

Agriculture, Ecosystems and Environment

A predator in need is a predator indeed: generalist predators (spiders and ladybeetles) specialize in pest consumption at the late growth stage of rice

--Manuscript Draft--

Manuscript Number:	AGEE38266R1
Article Type:	Research Paper
Keywords:	Biocontrol; generalist predators; rice paddy; organic and conventional farms
Manuscript Region of Origin:	TAIWAN
Abstract:	<p>Biocontrol, using natural enemies for pest control, has a long history in agriculture. It has received a surge of interest in the recent Anthropocene because of its potential as a valuable tool for sustainable agriculture. To solve a long-standing puzzle in biocontrol—how well the ubiquitous generalist arthropod predators (GAPs) function as biocontrol agents—this study aimed to 1) quantify the diet composition of GAPs (spiders and ladybeetles) at different crop stages using stable isotope analysis, 2) examine the consistency of GAPs in pest consumption over years, and 3) investigate how abiotic and biotic factors affect pest consumption by GAPs. Specifically, we sampled arthropod prey and GAPs in sub-tropical organic and conventional rice farms over crop stages (seedling, tillering, flowering, and ripening) in three consecutive years. Among our field-collected samples, 352 arthropod predator and 828 prey isotope samples were analyzed to infer predator-prey interactions. Our results show the following: a) The proportion of rice pests in GAPs' diets in both organic and conventional rice farms increased over the crop season, from 21-47% at the tillering stage to 80-97% at the ripening stage, across the three study years. The high percentage in pest consumption at late crop stages (flowering and ripening) suggests that GAPs can function as specialists in pest management during the critical period of crop production. Regarding individual predator groups, spiders and ladybeetles exhibited distinct dietary patterns over crop stages. b) The high pest consumption by GAPs at late crop stages was similar across years despite variable climatic conditions and prey availability, suggesting a consistency in GAP feeding habits and biocontrol value. c) The proportion of rice pests in GAPs' diets varied with farm type and crop stage (e.g., higher in conventional farms and during flowering/ripening stages). By quantifying the diet composition of GAPs over crop stages, farm types, and years, this study reveals that generalist predators have potential to produce a stable, predictable top-down effect on pests in rice agro-ecosystems. As sustainable agriculture has become increasingly important, incorporating the ubiquitous generalist predators into pest management will likely open a promising avenue towards this goal.</p>



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December 4, 2023

Dear Dr. Audrey Alignier and Editorial Board Members,

Thank you for inviting us to submit a revised version of our manuscript (AGEE38266R1) to *Agriculture, Ecosystems and Environment*. We appreciate the constructive comments from you and the reviewers. We have carefully considered each comment, and our point-by-point responses are provided in this letter.

For clarity, each reviewer's comment is attached below (in gray highlight) and followed by our reply. Line numbers in our reply refer to the revised version with tracked changes unless otherwise mentioned. Besides the official files submitted to the AGEE website, we also provide these two files with tracked changes in our Google Drive for your information. For clarity, AGEE Editorial Office asked us to remove these files from the submission system:

1. Manuscript to AEE 2023-1204 Main text (track changes)

The main text with tracked changes.

<https://drive.google.com/file/d/1jxhhAUUpNpQaKifmllrzuVncRqg7LfNuT/view?usp=sharing>

2. Manuscript to AEE 2023-1204 Highlights (track changes)

The highlights with tracked changes.

<https://drive.google.com/file/d/1zPLhBU3VTbUEHYa8rhQluLx8KyEub1ST/view?usp=sharing>

Our study helps solve a long-standing puzzle (the role of generalist predators such as spiders and ladybeetles in pest management) by using stable isotopes to quantify arthropod predators' diet composition over crop stages, farm types, and years. Therefore, our findings should be of interest to a wide range of ecologists, agricultural practitioners, and policy makers. We believe that the revisions based on review comments have improved the quality of this manuscript, and we hope that the manuscript is now suitable for publication in *Agriculture, Ecosystems and Environment*.

Sincerely,

Chuan-Kai Ho
Professor
Institute of Ecology and Evolutionary Biology
National Taiwan University

The following includes our replies to these four sections of comments:

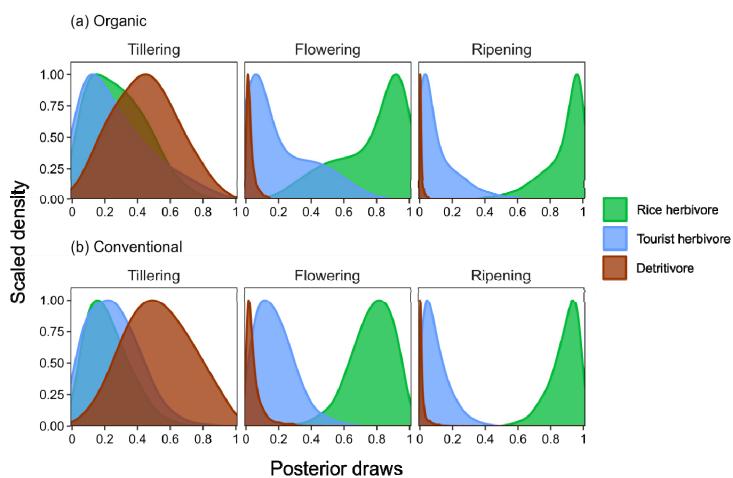
- Editor's comments
- Reviewers' comments
- Reviewer 1's comments
- Reviewer 2's comments

Editor's comments

Thanks for your submission of a manuscript AGEE38266 titled 'A predator in need is a predator indeed: generalist arthropod predators function as pest specialists at the late growth stage of rice'. The manuscript has been reviewed by two independent experts. As you will see from their comments copied below, reviewers find the topic of interest for AGEE readership. However, Reviewer#1 raised major concerns that I agree with especially about a better presentation of data on which tests were performed. Please consider presenting data in form of tables of medians and credible interval rather than means and standard errors; and for figures in form of posterior density plots rather than linear graphs. You must also better argue for the appropriateness of MixSIAR models. I also suggest to carefully edit the manuscript (1.219 : tillering ? and 1.247 : tilling instead of tillering ?). Avoid to call for figures in the discussion section (main figures are more commonly associated with results). When revising your manuscript, please consider all issues mentioned in the reviewers' comments carefully. Outline every change made in response to their comments and provide suitable rebuttals for any comments not addressed.

[Reply] We thank the constructive comments from the editor and reviewers. We briefly summarize our responses below. More details are provided in our point-by-point responses to reviewers' comments.

- 1) *Table of posterior estimates* As suggested, we now provide a table of posterior means, posterior SDs, posterior medians, and 95% credible intervals for the proportion of prey sources in predators' diet (Appendix B). Note that this table includes 711 rows of data (with rice herbivores, tourist herbivores, and detritivores as prey sources) and will result in 237 posterior density plots (figures). Below we just list six posterior density plots from this study as examples.



- 2) *Posterior density plots vs. linear graphs* It may not be easy for our readers to digest 237 posterior density plots and generate a conclusion. To solve this issue and demonstrate the most important results, we extracted the posterior medians (a key suggestion from the last round of review) from the Bayesian stable isotope mixing models, calculated the SEs for the posterior medians, and presented the results (e.g., Figure 1). While there might be other ways to present the results, linear graphs (e.g., Figure 1) offer a good option to summarize hundreds of posterior density plots in a simple way and also reflect the time series survey in this study (i.e., different crop stages).
- 3) *Appropriateness of MixSIAR models* Thanks for asking this question. We are confident about the MixSIAR models in this study because of these reasons: a) We actually consulted one of the MixSIAR creators, Dr. Brian Stock, during our data analysis. b) The MixSIAR model estimation in this study is suitable because the three prey sources exhibit distinct isotope signatures in the isotopic space (Appendix A: Fig. S1). c) Our model convergence is assessed via Gelman-Rubin and Geweke diagnostics (Line 198). The diagnostics show that all of our mixing models have converged, further suggesting the appropriateness of the MixSIAR models in this study.
- 4) *Tillering vs. tilling* a) Thanks for raising this issue. Tillering is the appropriate term in this study. “Tillering” refers to the stage when plants start to branch rapidly. “Tilling” means to prepare the land for growing crops. b) We have checked the manuscript thoroughly and corrected one typo in Line 254.
- 5) *Figures in Discussion* Originally we provided figure and table numbers in Discussion to facilitate our readers to locate relevant results. As suggested, we now remove this information except for Appendix figures and figure comparisons.

Reviewers' comments

1. Are the objectives and the rationale of the study clearly stated? Please provide suggestions to the author(s) on how to improve the clarity of the objectives and rationale of the study. Please number each suggestion so that author(s) can more easily respond.

Reviewer #1: Yes. More clear now

Reviewer #2: Yes.

[Reply] We appreciate the positive comments.

2. If applicable, is the application/theory/method/study reported in sufficient detail to allow for its replicability and/or reproducibility? Please provide suggestions to the author(s) on how to improve the replicability/reproducibility of their study. Please number each suggestion so that the author(s) can more easily respond.

Reviewer #1: Mark as appropriate with an X:

Yes No N/A

Provide further comments here:

- 2.1) The Bayesian mixing model MixSIAR works primarily within the framework of comparing relative importance of various food source options in consumers' diets. While the model would work well for the herbivore food sources in predator diets (since we have multiple herbivores in the study), it is hard to see how it worked for herbivores as consumers given that only rice was considered as a source for herbivores.

[Reply] Yes, if a study aims to analyze the diet composition for herbivores (e.g., generalist herbivores), it will need to include multiple plant sources.

- 2.2) The authors also need to state the sources of the means and standard deviation values of the various food sources (usually mandatory) that they applied to the MixSIAR models, and why they think these were appropriate for their particular study context

[Reply] Please find this information in the stable isotope biplot (mean and 95% CI) for the three prey sources of this study (Appendix A: Fig. S1). Our models should be appropriate because a) the three prey sources exhibit distinct isotope signatures in the isotopic space (Appendix A: Fig. S1), and b) our models pass the Gelman-Rubin and Geweke's convergence diagnostics.

- 2.3) In disputing the suggestion that a 1-km buffer is too large for most low-mobility arthropods with regards to trophic linkages, the authors refer to Rusch 2016 and Karp 2018 to maintain their stance. However, the two references relate to landscape-scale rather than plot-level or farm-level contexts which is the case for the present study. Also the full reference for Karp is not included in the bibliography

[Reply]

- a) Thank the reviewer for pointing out this. We now add Karp et al. (2018) to our reference. Therefore, both Rusch et al. (2016) and Karp et al (2018) are included in our reference:

Rusch, A., Chaplin-Kramer, R., Gardiner, M.M., Hawro, V., Holland, J., Landis, D., Thies, C., Tscharntke, T., Weisser, W.W., Winqvist, C., 2016. Agricultural landscape simplification reduces natural pest control: A quantitative synthesis. *Agriculture, Ecosystems & Environment* 221, 198-204.

Karp, D.S., Chaplin-Kramer, R., Meehan, T.D., Martin, E.A., DeClerck, F., Grab, H., Gratton, C., Hunt, L., Larsen, A.E., Martínez-Salinas, A., 2018. Crop pests and predators exhibit inconsistent responses to surrounding landscape composition. *Proceedings of the National Academy of Sciences* 115, E7863-E7870.

- b) We agree that there is no universal consensus on the buffer zone. The 1-km radius in this study was based on previous studies (Rusch et al., 2016; Karp et al. 2018). In fact, Rusch et al. (2016) stated in their methods section that "The 1 km spatial extent was selected because it has been identified as a relevant scale to understand trophic interactions and population

dynamics for a range of organisms including natural enemies of crop pests (Thies and Tscharntke, 1999, Thies et al., 2005)". Therefore, we decided to use a 1-km radius to evaluate the effect of surrounding forest cover on each study farm.

2.4) Like Reviewer#1 pointed out, and so did I in my initial review, the role of years on observed trends seems irrelevant, given that, firstly, agronomic practices on rice-fields of Taiwan are the same always and, secondly, years are not ecological variables such as habitat characteristics. The influence of years thus needs to be omitted completely, and instead use samples per year as replicates on the temporal scale. Implying observed trends across years to be indicators of potential use for climate tracking (as laid out in the Highlights) is too far-fetched. As the presented data from the GLM test show, year was not important as a factor anyway.

[Reply] 

- a) As mentioned in our introduction and discussion sections, many abiotic and biotic factors (e.g., precipitation and pest population, respectively) can change from year to year. Therefore, it is interesting and important to examine whether pest consumption patterns vary with years. While the statistical analysis shows that year per se is not statistically significant, this result is meaningful to the field of predator-prey interactions and pest management.
- b) That being said, we understand the reviewer's concern about the conclusions based on three years of climatic data. Therefore, we have toned down our conclusions and revised the highlight, abstract, and conclusion sections accordingly.

2.5) In response to the query regarding use of spiders and lady beetles to generalize for all generalist predators, the authors argue that these two are considered common and thus representative of all generalist predators. This is not only wrong, given the diversity in foraging patterns amongst farmland predator groups, but also is compounded in this study by the various dimensions of explanatory factors: different farming systems; across multiple year; crop stages; vegetation structure; temperature etc. A further potential confounding element is, as reviewer# pointed out, the phenomenon of intra-guild predation, which many spiders are known for. In any case if the criterion was commonness, than ants are far more ubiquitous in all farming habitats than spiders and beetles, both on spatial as well as temporal scales. Why were ants left out?

[Reply] Thanks for the comments. We address each concern below:

- a) *Spiders and ladybeetles* This study haphazardly sampled arthropods in rice farms and analyzed the most abundant generalist predators, rice herbivores, tourist herbivores, and detritivores. Spiders and ladybeetles (7 families in total) were found to be the most abundant generalist arthropod predators in our study farms (Line 171). Other arthropod predators (lacewings, assassin bugs, earwigs, ground beetles, etc.) were rare or absent. This pattern (spider and ladybeetle dominance) is also supported by an independent study conducted by the Hualien District Agricultural Research and Extension Station in Taiwan (*personal communications*). To avoid over-generalizing our results, we have clarified that the results

are based on spiders and ladybeetles in this manuscript. If there is still a room to improve, we welcome any constructive suggestions.



- b) *Ants* While ants are important in some ecosystems, they were rare in our rice farms, likely due to rice irrigation practices. We consulted an ant expert in Taiwan (Dr. Feng-Chuan Hsu) and learned that *Nylanderia yaeyamensis*, *Tapinoma melanocephalum*, *Pheidole megacephala* and *Paratrechina longicornis* may be found occasionally at low population densities in rice paddies in Taiwan. These ant species do not prefer irrigated habitat.
- c) *Intraguild* We speculate that intraguild predation (IGP) may not be a major concern in our study system because rice plants grow in dense clumps and form a complex structure that could substantially reduce IGP pressure (Line 393). However, we do acknowledge this limitation (i.e., IGP absence in MixSIAR models) in the *Potential caveats of this study* section of our discussion.
-

- 2.6) In categorizing detritivores, the authors list some grasshopper groups, but leave out crickets. This is a bit worrying, given that crickets are among the most common detritivores (they are also omnivores) in rice farming systems. It is not reasonable for the authors to argue that crickets were excluded because they were rare in the farms studied

[Reply] Thanks for asking this question. We ~~haphazardly~~ sampled arthropods and did not leave any species intentionally. Crickets were rarely found in our rice paddies likely because these paddies were irrigated frequently.

- 2.7) Also stating (retroactively) that only Hemiptera that consumed plant material were combined with grasshoppers for stable isotope analyses, without specifying which these were (after earlier stating that such combinations was done indiscriminately) only serves to raise suspicion about the data and analytical soundness for this study.

[Reply] a) The stable isotope samples of Hemiptera (*Nephrotettix*, *Nilaparvata*, *Pachybrachius*, and *Scotinophara*) and Orthoptera (*Atractomorpha* and *Acrididae*) were analyzed separately. b) They belong to either rice herbivores or tourist herbivores in our MixSIAR models. Please see details in Appendix A (Table S1).

Reviewer #2: Mark as appropriate with an X:

Yes No N/A

Provide further comments here:

- 2.8) L. 156. It is unclear how were the samples for the isotopic analyses made. Were all collected arthropods included in the samples or it was representative sub-samples that mirrored the composition proportionally?

[Reply] Thanks for raising this issue. Yes, we used sub-samples that mirrored the arthropod community composition in the field. We now add this information in Methods (2.2. *Stable isotope analysis of arthropod samples*).

3. If applicable, are statistical analyses, controls, sampling mechanism, and statistical reporting (e.g., P-values, CIs, effect sizes) appropriate and well described? Please clearly indicate if the manuscript requires additional peer review by a statistician. Kindly provide suggestions to the author(s) on how to improve the statistical analyses, controls, sampling mechanism, or statistical reporting. Please number each suggestion so that the author(s) can more easily respond.

Reviewer #1: Mark as appropriate with an X:

Yes No N/A

Provide further comments here:

3-1) Good that beta regression with logit link function is now included in the analysis (Table 1). This is ok for the present purposes, even though beta regression would usually be most elegant for binary datasets. It is ok for here due to the use of logit (rather than log) link. Still, it is curious why, according to results of GLM analyses, Year was an important variable driving lady beetle predation rate.

[Reply] We appreciate the comments. Honestly, we do not know why year played a role in ladybeetles' diet composition. A possibility is that ladybeetles may prefer certain preys that happened to vary with years.

3-2) If the authors have significant challenges handling MixSIAR modeling tools, it may be reasonable for them to call in technical support, or consider analyzing their data using alternative tools such as those involving molecular markers, specifically DNA meta-barcoding. However, while this will provide a thoroughly detailed resolution of trophic linkages (including at specie level), it will not estimate relative importance of food items in consumer diets the way MixSIAR can. Furthermore, DNA meta-barcoding would involve re-testing all the samples in the laboratory, with the obvious cost and time implications.

[Reply] Thanks for this suggestion. As mentioned in our reply to the editor, we consulted one of the MixSIAR creators, our prey sources exhibited distinct isotope signatures, and our models passed the Gelman-Rubin and Geweke's convergence diagnostics. Therefore, we are confident about the appropriateness of our MixSIAR models. We agree that molecular gut content analysis will be another approach to study trophic interactions, although it has its limitation (e.g., a "snapshot" technique) and may not serve the purpose of this study (Line 129).

3-3) Like Reviewer#1, I have concerns as to why conclusions are drawn on observations from 4 crop stages yet results are presented inconsistently for 3 or 2 crop stages only growth stages. Was there anything wrong with data sets?

[Reply] We collected arthropod samples at four crop stages over the rice growth season and prepared isotope samples for all crop stages. However, there were not enough data points at the seedling stage for stable isotope mixing model estimation. Therefore, we excluded this stage in the subsequent diet composition and beta regression analyses (Line 192). This is why there are only three crop stages (tillering, flowering, and ripening) in Table 3 (Tukey's post-hoc tests for pest consumption among crop stages), Fig. 1 (diet composition of predators over the crop season),

and Fig. 2 (pest consumption by predators over the crop season), but four crop stages (seedling, tillering, flowering, and ripening) in Fig. 3 (relative abundance of prey sources over the crop season).

3-4) With reference to Table 2 and Table 3: Tukey post-hoc tests are supposed to be POST-HOC tests of some original analytical procedures to resolve which factors has the greater weights than some other(s) one(s) in determining results obtained in ANOVA etc. Where are these original test results? Besides, Tukey post-hoc test results should return test statistics, p-values and degrees of freedom. Where are these in Table 2 and Table 3 results here?

[Reply] The original beta GLM model results were shown in Table 1. Because farm type and crop stage were significant (for “Both predators”), we proceeded to conduct Tukey’s post-hoc comparisons of the predictor levels using the R package “emmeans”. We used a critical value approach with $\alpha = 0.05$ for the post-hoc tests, and therefore no degrees of freedom and p-values were returned. Instead, the level differences were evaluated based on the confidence intervals adjusted for multiple comparisons (as shown in Table 2 and 3).

Reviewer #2: Mark as appropriate with an X:

Yes No N/A

Provide further comments here:

3-5) The authors state that the design was paired (L. 132-136), nevertheless they did not account for the paired design in their statistical analyses as GLMs were used (L. 199). Instead GLMMs should be used with the pair ID as the random effect. Moreover, for me it is unclear whether the same fields or different fields were sampled across the three years. If the same fields were used, then the random effects should be field id nested within pair id.

[Reply] Thanks for this constructive suggestion. We have re-run the beta regression models with farm ID nested within pair ID as random effects and updated the methods (Line 206) and results (Line 258-273) accordingly. Note that this does not change our conclusions.

4. Could the manuscript benefit from additional tables or figures, or from improving or removing (some of the) existing ones? Please provide specific suggestions for improvements, removals, or additions of figures or tables. Please number each suggestion so that author(s) can more easily respond.

Reviewer #1: The current tables and figures present results of means and standard errors and line graphs yet for food proportions, these should be changed to median and credible intervals for tables, and probability density plots for figures. At least 1 table with isotopic signature values for consumers and food sources is also necessary at least as a supplementary material

Reviewer #2: No.

[Reply]

- a) As suggested, we now provide a table of posterior means, posterior SDs, posterior medians, and 95% credible intervals for the proportion of prey sources in predators' diet (Appendix B).
 - b) Note that the aforementioned table includes 711 rows of data (with rice herbivores, tourist herbivores, and detritivores as prey sources), which will generate 237 posterior density plots (figures). To summarize this large number of plots, we extracted the posterior medians from the Bayesian stable isotope mixing models (suggested in the last round of review), calculated the SEs for the posterior medians, and presented the results in linear graphs (e.g., Figure 1). This should be a good way to help readers visualize the model results compared to browsing hundreds of posterior density plots.
 - c) We provide a stable isotope biplot (Appendix A: Fig. S1) to show the stable isotope signatures of different prey sources in this study. Their distinct isotope signatures in the isotopic space support the use of MixSIAR models in this study. Since there are hundreds of predator signatures for different species-year-farm-crop stage combinations, predator data are now shown in this biplot. However, if anyone requests, we are more than happy to provide the raw data for stable isotope signatures.
5. If applicable, are the interpretation of results and study conclusions supported by the data? Please provide suggestions (if needed) to the author(s) on how to improve, tone down, or expand the study interpretations/conclusions. Please number each suggestion so that the author(s) can more easily respond.

Reviewer #1: Mark as appropriate with an X:

Yes No N/A

Provide further comments here:

- 5.1) Spiders and ladybirds should not be construed to represent all generalist predators even if they are very common in rice-fields. Ants are more common than all the rest, yet they are not included here

[Reply] We agree with the reviewer that spiders and ladybeetles do not represent all generalist predators. We have revised the manuscript accordingly to avoid over-generalization. Regarding ants, please see our reply above (Reviewers' comment 2.5).

- 5.2) Observed yearly trends in the results should not be taken to imply corresponding climatic trends

[Reply] We agree that three years of climatic data may not be enough to provide conclusive evidence. Therefore, we now avoid this inference in our highlights and manuscript.

Reviewer #2: Mark as appropriate with an X:

Yes No N/A

Provide further comments here:

6. Have the authors clearly emphasized the strengths of their study/theory/methods/argument? Please provide suggestions to the author(s) on how to better emphasize the strengths of their study. Please number each suggestion so that the author(s) can more easily respond.

Reviewer #1: 1. the main strength of the study is in the use of stable isotopes to quantify trophic linkages in arthropods of rice-fields, which is novel, and in the characterization of the role of crop stages. But the authors seem to emphasize only the predation specialization aspect, which was not strongly supported by the study design and analytical procedures

Reviewer #2: Yes.

[Reply] Thanks for the positive comments. As suggested, we have updated our analysis and avoided over-generalization. Please see our reply above for more details.

7. Have the authors clearly stated the limitations of their study/theory/methods/argument? Please list the limitations that the author(s) need to add or emphasize. Please number each limitation so that author(s) can more easily respond.

Reviewer #1: Yes

Reviewer #2: Yes.

[Reply] We appreciate the positive comments.

8. Does the manuscript structure, flow or writing need improving (e.g., the addition of subheadings, shortening of text, reorganization of sections, or moving details from one section to another)? Please provide suggestions to the author(s) on how to improve the manuscript structure and flow. Please number each suggestion so that author(s) can more easily respond.

Reviewer #1: Generally yes,

Reviewer #2: No.

[Reply] Thanks for the positive comments.

9. Could the manuscript benefit from language editing?

Reviewer #1: No

Reviewer #2: No

[Reply] Thanks for the positive comments.

Reviewer 1's comments

Title

The authors have made no attempt to modify any part of the title, in light of changes earlier suggested, and in light of their own admission that they focused on two predator groups

rather than all generalist predators. Suggested title: "Spiders and lady-beetles consume higher proportions of rice pests at late growth stages regardless of farming system"

[Reply] We have modified the title to include the reviewer's feedback (spiders and ladybeetles as key words for clarification) and keep the focus of this study (generalist arthropod predators). The new title is "A predator in need is a predator indeed: generalist predators (spiders and ladybeetles) specialize in pest consumption at the late growth stage of rice".

The Highlights

- * The authors have made no changes to the here, in light of changes earlier suggested for study design, data analyses and results or conclusion.
- * Observations across the three years cannot reasonably be used to imply the role of climate change in Taiwan

[Reply] As suggested, we have updated the highlights, data analysis, results, and conclusions.

Abstract

The authors have made absolutely no changes to the abstract, in light of changes earlier suggested for study design, data analyses and results or conclusion

[Reply] As mentioned above, we have revised our manuscript accordingly.

Reviewer 2's comments

L. 207. Why only forest habitats and not also other habitat types?

[Reply] This is because the landscape types surrounding our study farms are mostly farmlands and forests. Therefore, we examined the forest habitats to understand their potential effect on our study farms.

L. 211. Spiders can use the sit-and-move and active hunting too. For example, oxyopids and clubionids that were included in the analyses (TableS1) do not use sit-and-wait. Oxyopids use sit-and-move strategy while clubionids use active hunting. Just use different justification.

[Reply] Thanks for pointing this out. As suggested, we now remove the "sit-and-wait vs. active hunting" here. Please note that long-jawed orb-weavers (*Tetragnatha*) were the most abundant genus in our spider samples. Therefore, we mentioned their sit-and-wait foraging behavior vs. ladybeetles' active hunting behavior in Discussion (Line 322).

L. 270. Paddy fields instead of agro-ecosystems

[Reply] For clarify, we now use "rice agro-ecosystems" instead of "agro-ecosystems".

L. 283. Forest cover instead of surrounding landscape.

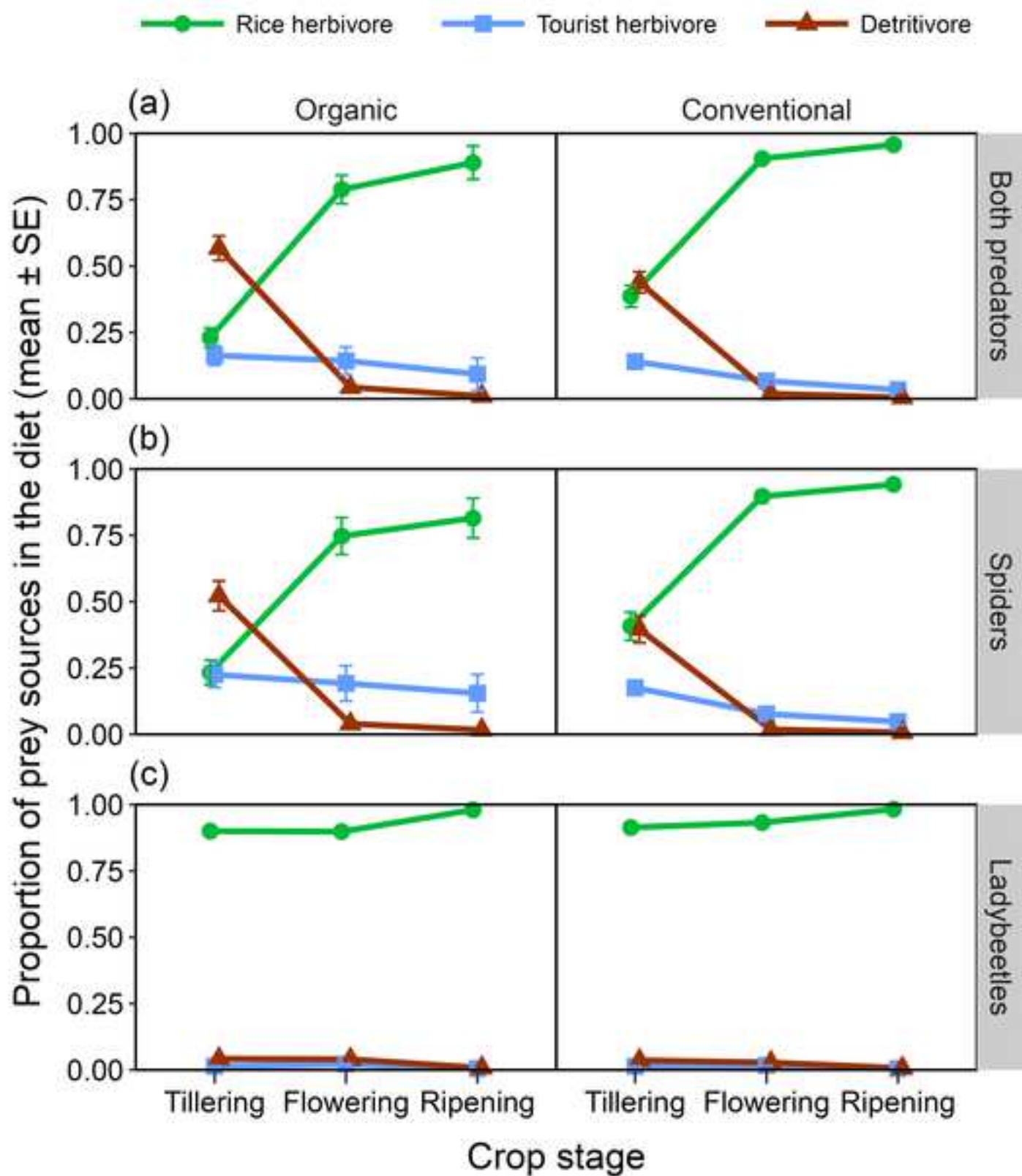
[Reply] We now use "percent forest cover" instead of "surrounding landscape".

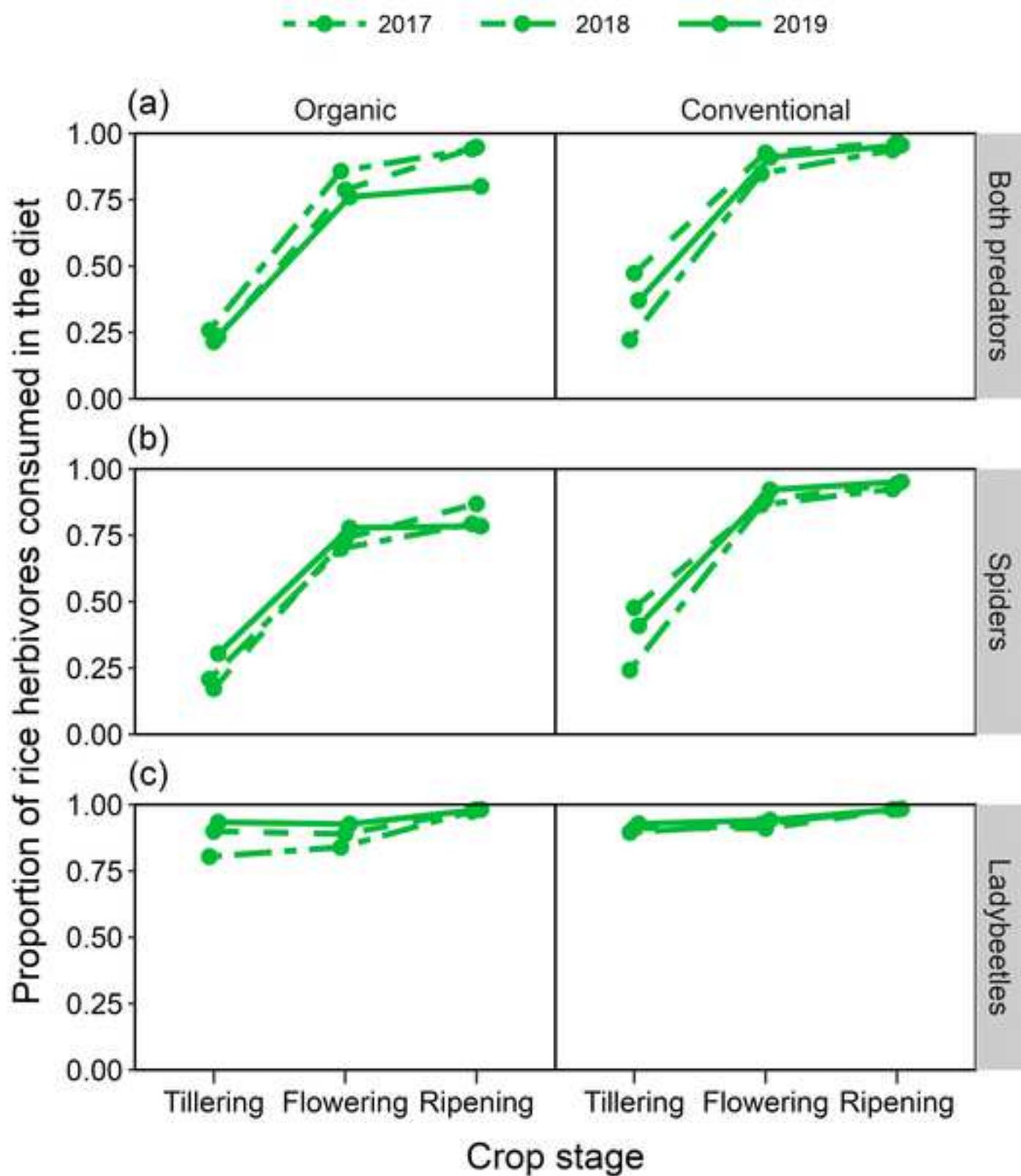
L. 380-381. Actually spiders are very effective in suppressing pests in rice fields in comparison to other crops and this study shed some light on why. See the meta-analysis Michalko et al. 2019, *Glob. Ecol. Biogeogr.* 28(9): 1366-1378.

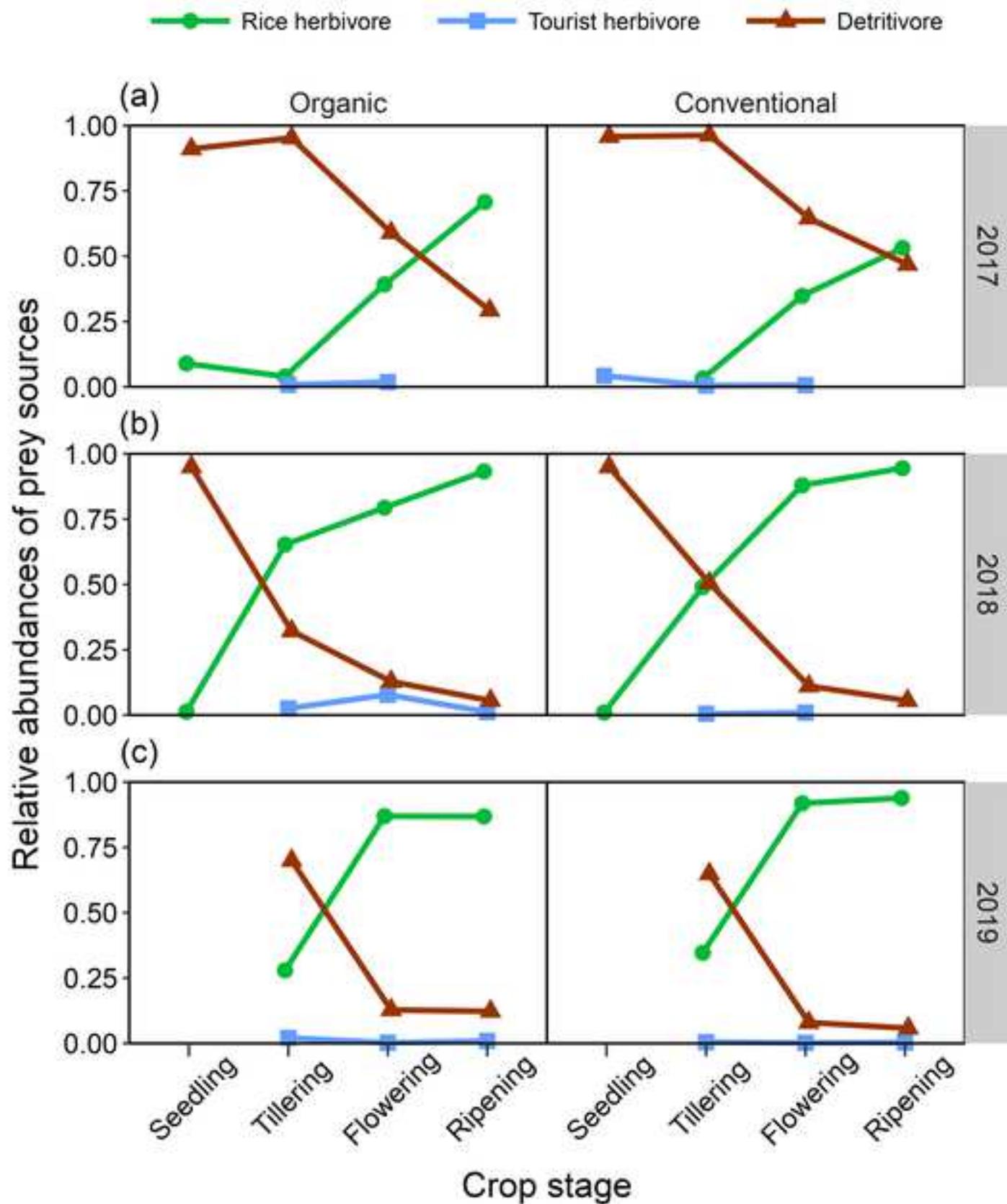
[Reply] Thanks for the positive comments. We also cited a similar work from Dr. Michalko in this manuscript (Line 69).

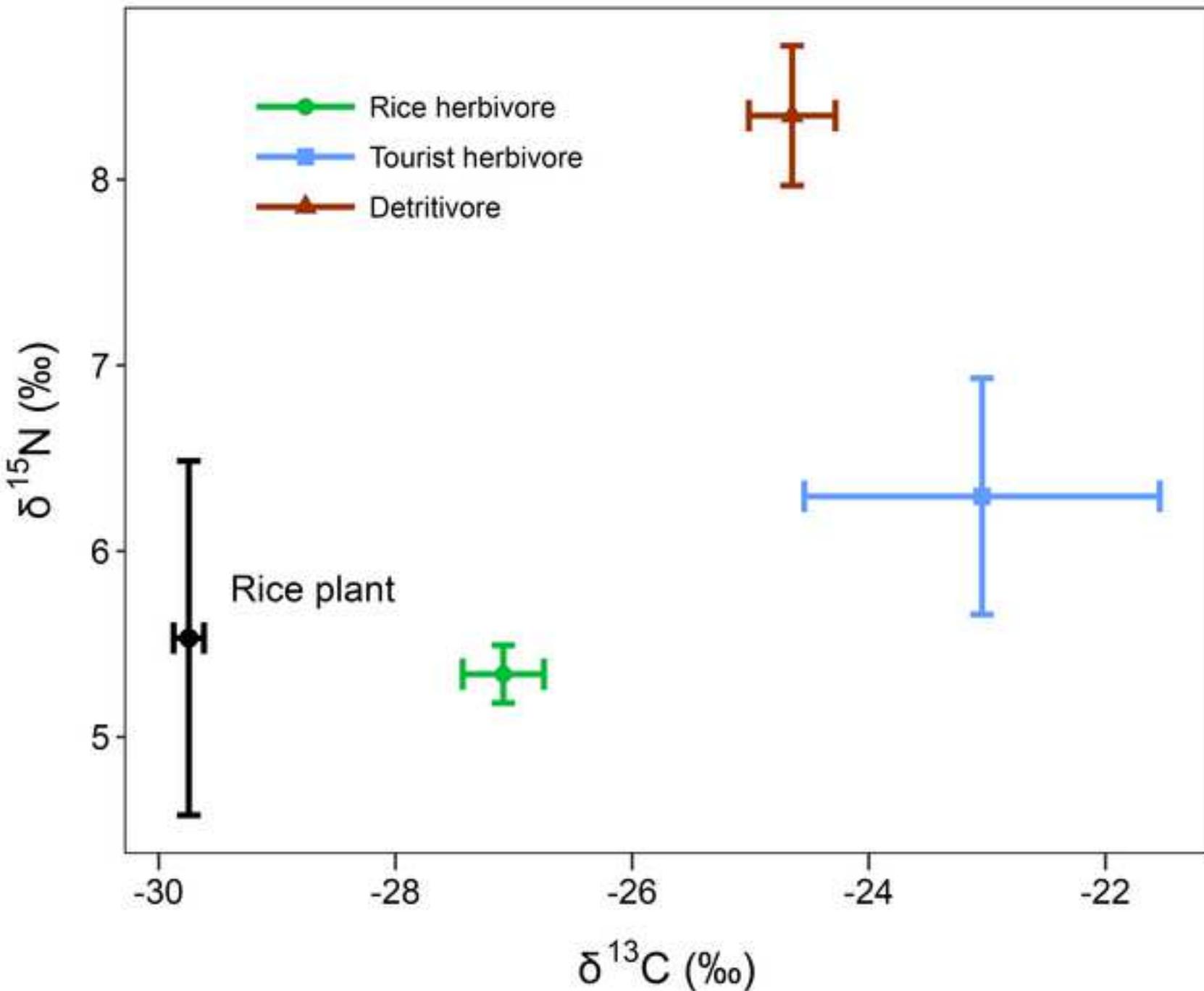
Highlights

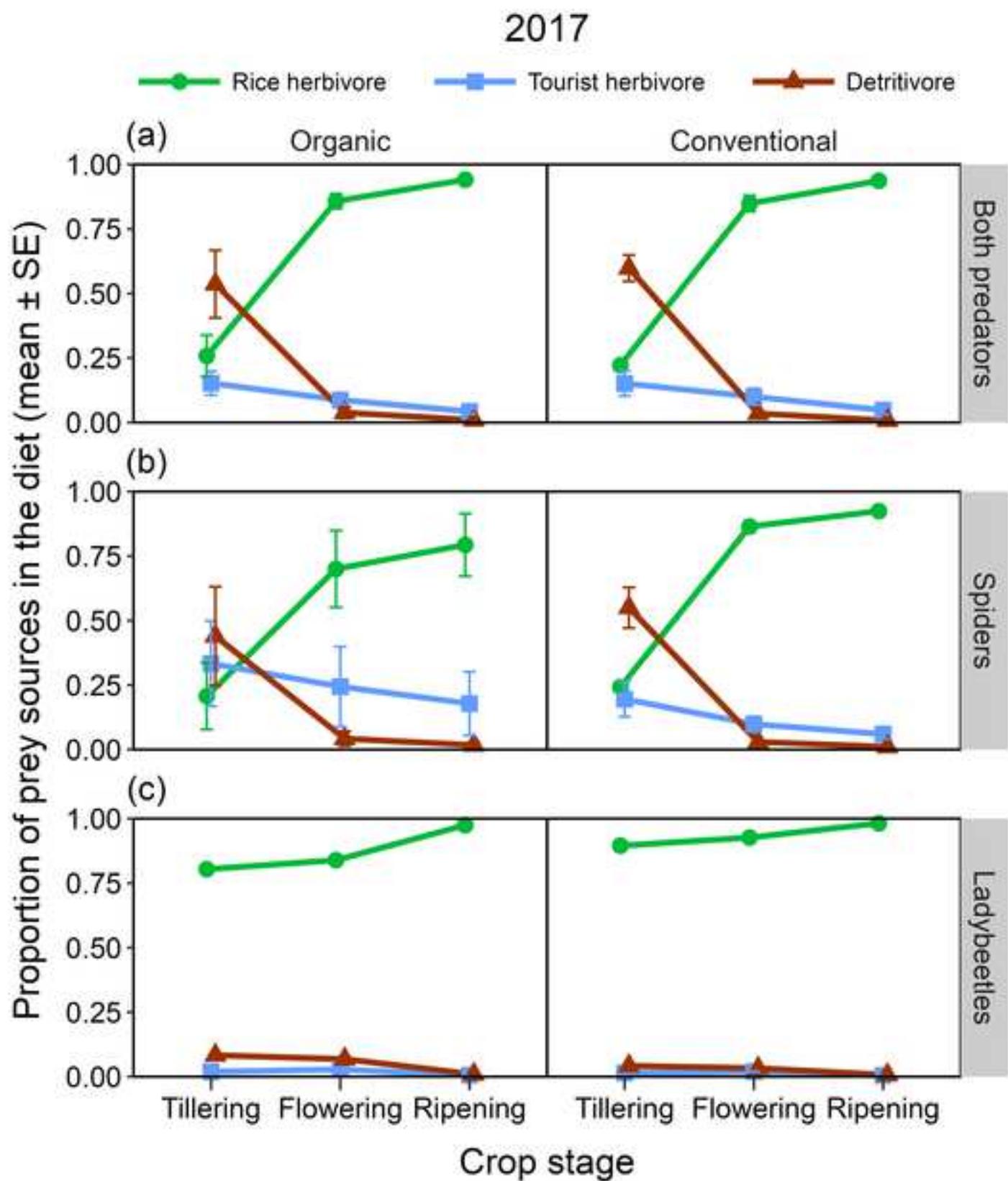
- We analyzed arthropod isotope samples in organic and conventional rice farms
- Generalist arthropod predators (GAPs) (spiders and ladybeetles) specialize in pest consumption at late crop stages
- The high pest consumption by GAPs is consistent across years and farms
- The results lend support to applying GAPs as biocontrol agents in agroecosystems

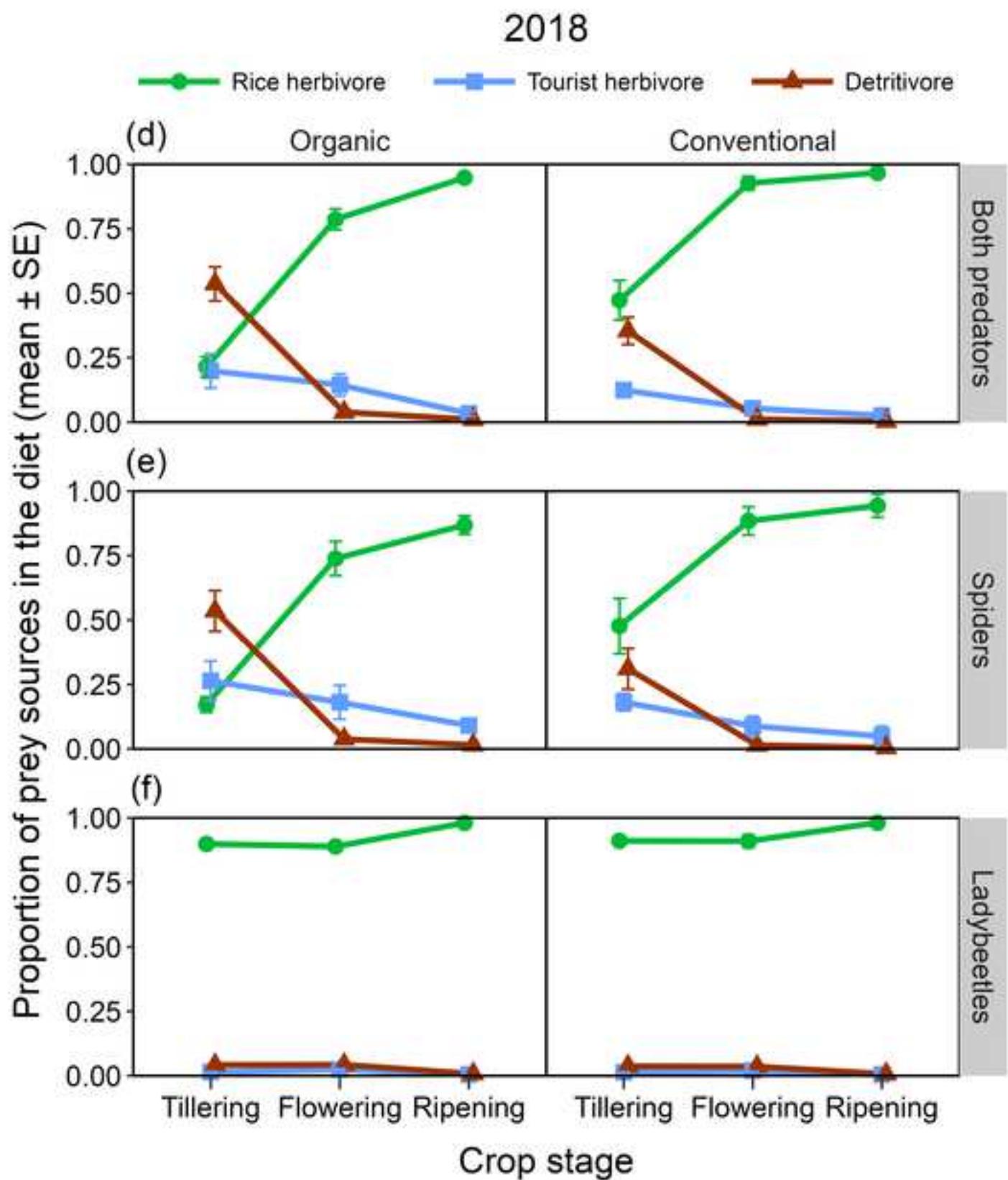












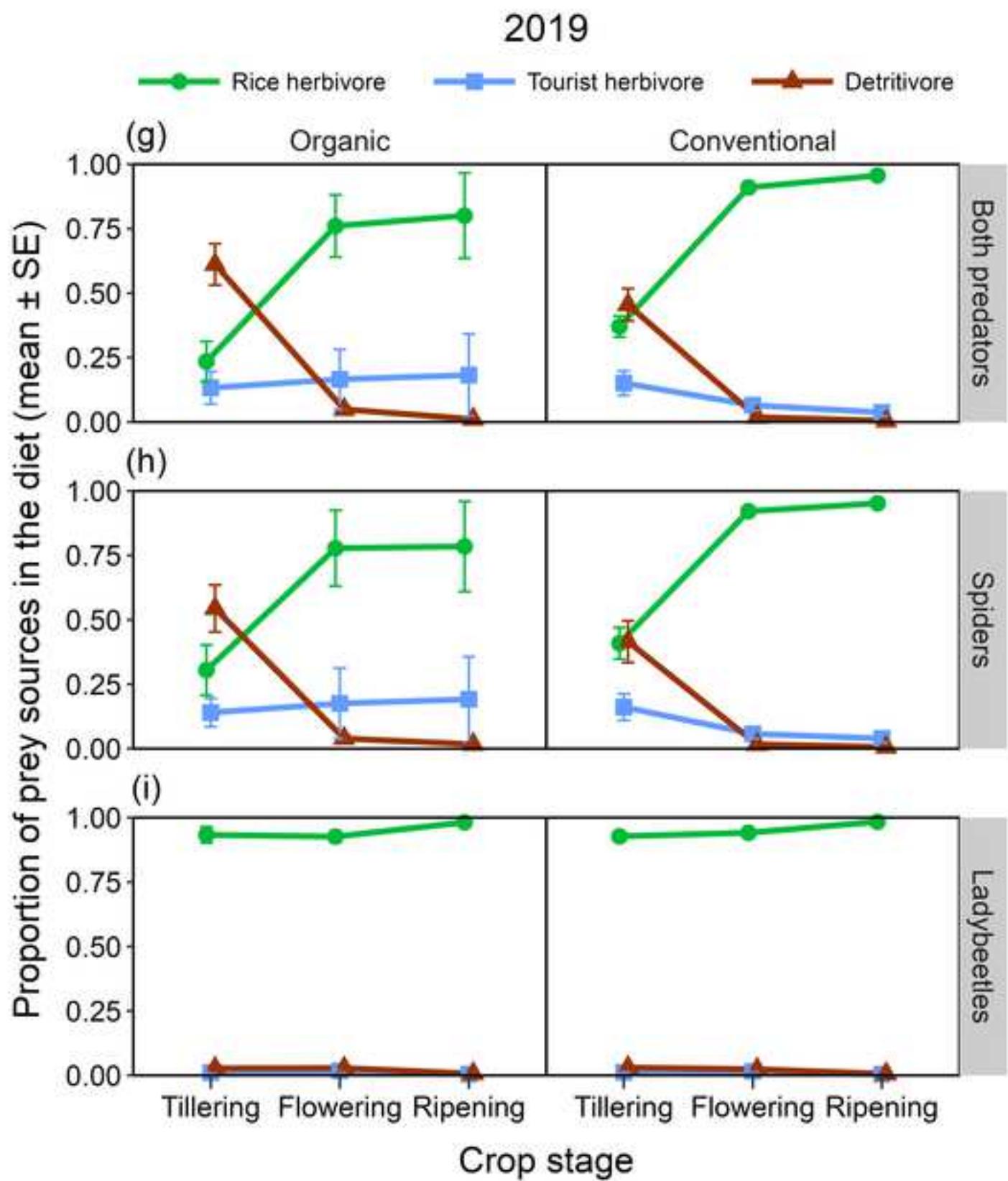
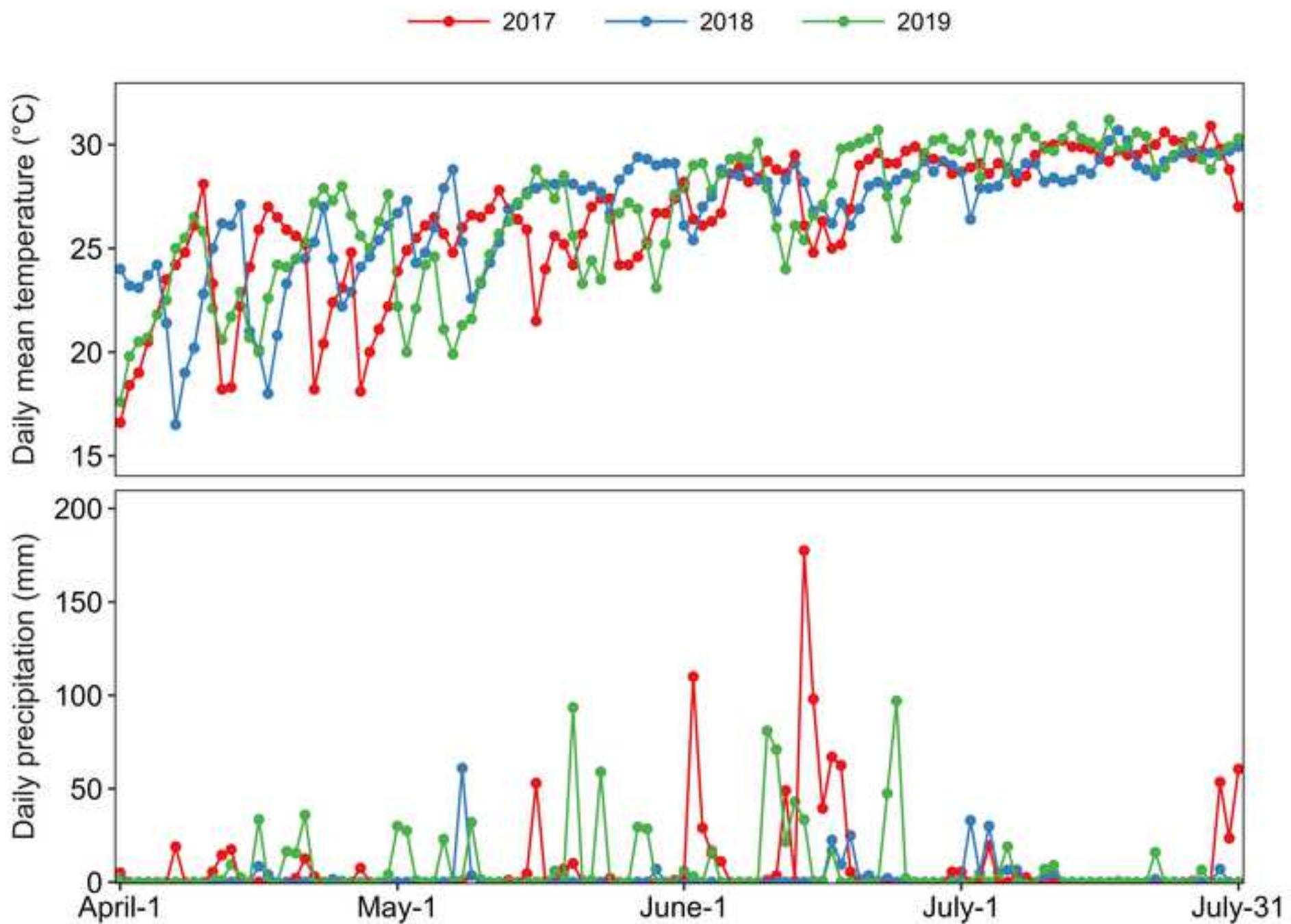


Figure S3

[Click here to access/download;Figure;Figure S3.tif](#)

Appendix A.

1

2 **A predator in need is a predator indeed: generalist predators (spiders and**

3 **ladybeetles) specialize in pest consumption at the late growth stage of rice**

5 Gen-Chang Hsu¹, Jia-Ang Ou^{2,3}, Min-Hsuan Ni², Zheng-Hong Lin² and Chuan-Kai Ho^{1,2*}

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16 **Table S1.** The taxonomic information and trophic guilds of the arthropod samples in the three
17 study years.

18 (a) Year 2017

Trophic guild	Order	Family/Genus
Predators	Araneae	Araneidae
	Araneae	Clubionidae
	Araneae	Oxyopidae
	Araneae	Tetragnathidae/ <i>Tetragnatha</i>
	Araneae	Thomisidae
	Coleoptera	Carabidae
Rice herbivores	Coleoptera	Coccinellidae
	Hemiptera	Cicadellidae/ <i>Nephrotettix</i>
	Hemiptera	Delphacidae/ <i>Nilaparvata</i>
	Hemiptera	Lygaeidae/ <i>Pachybrachius</i>
	Hemiptera	Pentatomidae/ <i>Scotinophara</i>
	Lepidoptera	Hesperiidae
Tourist herbivores	Lepidoptera	Pyralidae
	Lepidoptera	Nymphalidae
	Orthoptera	Pyrgomorphidae/ <i>Atractomorpha</i>
	Coleoptera	Chrysomelidae
	Orthoptera	Acrididae
Detritivores	Diptera	Chironomidae
	Diptera	Chloropidae
	Diptera	Ephydriidae
	Diptera	Muscidae
	Diptera	Sphaeroceridae
	Diptera	Stratiomyidae
	Diptera	Tephritidae

	Orthoptera	Tetrigidae	
19			
20	(b) Year 2018		
	Trophic guild	Order	Family/Genus
Predators			
		Araneae	Araneidae
		Araneae	Clubionidae
		Araneae	Oxyopidae
		Araneae	Tetragnathidae/ <i>Tetragnatha</i>
		Araneae	Thomisidae
		Coleoptera	Coccinellidae
Rice herbivores		Hemiptera	Alydidae/ <i>Leptocorisa</i>
		Hemiptera	Cicadellidae/ <i>Nephrotettix</i>
		Hemiptera	Delphacidae/ <i>Nilaparvata</i>
		Hemiptera	Lygaeidae/ <i>Pachybrachius</i>
		Hemiptera	Pentatomidae/ <i>Scotinophara</i>
		Lepidoptera	Hesperiidae
		Lepidoptera	Pyralidae
		Orthoptera	Pyrgomorphidae/ <i>Atractomorpha</i>
Tourist herbivores		Coleoptera	Chrysomelidae
		Orthoptera	Acrididae
Detritivores		Diptera	Chironomidae
		Diptera	Chloropidae
		Diptera	Ephydriidae
		Diptera	Muscidae
		Diptera	Sciomyzidae
		Diptera	Stratiomyidae
		Orthoptera	Tetrigidae

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22 (c) Year 2019

Trophic guild	Order	Family/Genus
Predators	Araneae	Araneidae
	Araneae	Clubionidae
	Araneae	Oxyopidae
	Araneae	Tetragnathidae/ <i>Tetragnatha</i>
	Araneae	Thomisidae
	Coleoptera	Coccinellidae
Rice herbivores	Diptera	Agromyzidae
	Hemiptera	Alydidae/ <i>Leptocorisa</i>
	Hemiptera	Cicadellidae/ <i>Nephrotettix</i>
	Hemiptera	Coreidae
	Hemiptera	Delphacidae/ <i>Nilaparvata</i>
	Hemiptera	Lygaeidae/ <i>Pachybrachius</i>
	Hemiptera	Miridae
	Hemiptera	Pentatomidae/ <i>Scotinophara</i>
	Hemiptera	Ricaniidae
	Lepidoptera	Hesperiidae
	Lepidoptera	Nymphalidae
	Lepidoptera	Pyralidae
Tourist herbivores	Orthoptera	Pyrgomorphidae/ <i>Atractomorpha</i>
	Coleoptera	Chrysomelidae
Detritivores	Orthoptera	Acrididae
	Diptera	Calliphoridae
	Diptera	Chironomidae
	Diptera	Chloropidae
	Diptera	Ephydriidae
	Diptera	Lauxaniidae
	Diptera	Muscidae

Diptera	Phoridae
Diptera	Platystomatidae
Diptera	Sarcophagidae
Diptera	Sciomyzidae
Diptera	Sphaeroceridae
Diptera	Stratiomyidae
Diptera	Tephritidae
Orthoptera	Tetrigidae
Orthoptera	Tridactylidae

24 **Table S2.** The proportions (mean \pm SE) of prey sources (rice herbivores, tourist herbivores, and
 25 detritivores) consumed in predators' diet in organic and conventional rice farms over crop stages
 26 in each study year. The mean proportions were computed from the Bayesian posterior medians
 27 of diet estimates in replicate farms; n represents the number of replicate farms. Note that the
 28 differences in n within the same study year were due to insufficient predator samples in some
 29 replicate farms.

Year	Farm type	Crop stage	Predator	Prey source			n
				Rice herbivore	Tourist herbivore	Detritivore	
2017	Organic	Tillering	Both	0.26 \pm 0.08	0.15 \pm 0.05	0.54 \pm 0.13	3
			Spiders	0.21 \pm 0.13	0.33 \pm 0.17	0.44 \pm 0.19	3
			Ladybeetles	0.80	0.02	0.08	1
		Flowering	Both	0.86 \pm 0.03	0.09 \pm 0.02	0.04 \pm 0.02	3
			Spiders	0.70 \pm 0.15	0.24 \pm 0.16	0.04 \pm 0.03	3
			Ladybeetles	0.84	0.03	0.07	1
		Ripening	Both	0.94 \pm 0.01	0.04 \pm 0.01	0.01 \pm 0.01	3
			Spiders	0.79 \pm 0.12	0.18 \pm 0.12	0.02 \pm 0.01	3
			Ladybeetles	0.97 \pm 0.01	0.01 \pm 0.00	0.01 \pm 0.00	3
2018	Conventional	Tillering	Both	0.22 \pm 0.02	0.15 \pm 0.05	0.60 \pm 0.05	3
			Spiders	0.24 \pm 0.01	0.20 \pm 0.07	0.55 \pm 0.08	3
			Ladybeetles	0.90	0.01	0.04	1
		Flowering	Both	0.85 \pm 0.03	0.1 \pm 0.03	0.03 \pm 0.01	3
			Spiders	0.86 \pm 0.02	0.1 \pm 0.03	0.03 \pm 0.01	3
			Ladybeetles	0.93 \pm 0.01	0.02 \pm 0.00	0.03 \pm 0.00	2
		Ripening	Both	0.94 \pm 0.02	0.05 \pm 0.02	0.01 \pm 0.00	3
			Spiders	0.92 \pm 0.02	0.06 \pm 0.02	0.01 \pm 0.00	3
			Ladybeetles	0.98 \pm 0.00	0.00 \pm 0.00	0.01 \pm 0.00	2
2018	Organic	Tillering	Both	0.21 \pm 0.04	0.20 \pm 0.07	0.54 \pm 0.07	7
			Spiders	0.17 \pm 0.03	0.26 \pm 0.08	0.54 \pm 0.08	7
			Ladybeetles	0.90 \pm 0.02	0.01 \pm 0.00	0.04 \pm 0.01	6
		Flowering	Both	0.79 \pm 0.04	0.14 \pm 0.04	0.04 \pm 0.01	6
			Spiders	0.74 \pm 0.07	0.18 \pm 0.07	0.04 \pm 0.01	5

2019	Conventional	Tillering	Ladybeetles	0.89 ± 0.01	0.02 ± 0.00
			Both	0.95 ± 0.01	0.03 ± 0.01
			Spiders	0.87 ± 0.04	0.09 ± 0.02
		Flowering	Ladybeetles	0.98 ± 0.00	0.00 ± 0.00
			Both	0.47 ± 0.08	0.12 ± 0.02
			Spiders	0.48 ± 0.11	0.18 ± 0.03
	Organic	Tillering	Ladybeetles	0.91 ± 0.01	0.01 ± 0.00
			Both	0.93 ± 0.03	0.05 ± 0.02
			Spiders	0.88 ± 0.05	0.09 ± 0.04
		Flowering	Ladybeetles	0.91 ± 0.03	0.02 ± 0.00
			Both	0.97 ± 0.01	0.03 ± 0.01
			Spiders	0.94 ± 0.04	0.05 ± 0.04
		Ripening	Ladybeetles	0.98 ± 0.00	0.00 ± 0.00
			Both	0.23 ± 0.08	0.13 ± 0.06
			Spiders	0.30 ± 0.10	0.14 ± 0.05
	2020	Tillering	Ladybeetles	0.93 ± 0.03	0.01 ± 0.00
			Both	0.76 ± 0.12	0.17 ± 0.12
			Spiders	0.78 ± 0.15	0.18 ± 0.14
		Flowering	Ladybeetles	0.93 ± 0.02	0.02 ± 0.00
			Both	0.80 ± 0.17	0.18 ± 0.16
			Spiders	0.78 ± 0.17	0.19 ± 0.16
		Ripening	Ladybeetles	0.98 ± 0.00	0.00 ± 0.00
			Both	0.37 ± 0.04	0.15 ± 0.05
			Spiders	0.41 ± 0.06	0.16 ± 0.05
	2021	Tillering	Ladybeetles	0.93 ± 0.00	0.01 ± 0.00
			Both	0.91 ± 0.02	0.06 ± 0.02
			Spiders	0.92 ± 0.02	0.06 ± 0.02
		Flowering	Ladybeetles	0.94 ± 0.00	0.02 ± 0.00
			Both	0.96 ± 0.01	0.04 ± 0.01
			Spiders	0.95 ± 0.02	0.04 ± 0.02
		Ripening	Ladybeetles	0.98 ± 0.00	0.00 ± 0.00
			Both	0.37 ± 0.04	0.46 ± 0.06
			Spiders	0.41 ± 0.06	0.42 ± 0.08
		Tillering	Ladybeetles	0.93 ± 0.00	0.03 ± 0.00
			Both	0.91 ± 0.02	0.02 ± 0.00
			Spiders	0.92 ± 0.02	0.02 ± 0.01
		Flowering	Ladybeetles	0.94 ± 0.00	0.02 ± 0.00
			Both	0.96 ± 0.01	0.04 ± 0.01
			Spiders	0.95 ± 0.02	0.04 ± 0.02
		Ripening	Ladybeetles	0.98 ± 0.00	0.01 ± 0.00
			Both	0.37 ± 0.04	0.01 ± 0.00
			Spiders	0.41 ± 0.06	0.01 ± 0.00

31 **Table S3.** The relative abundance of the major families/genera in rice herbivore guild at the
32 flowering and ripening stages in the three study years. Samples were pooled across replicate
33 farms.

34 (a) Flowering stage

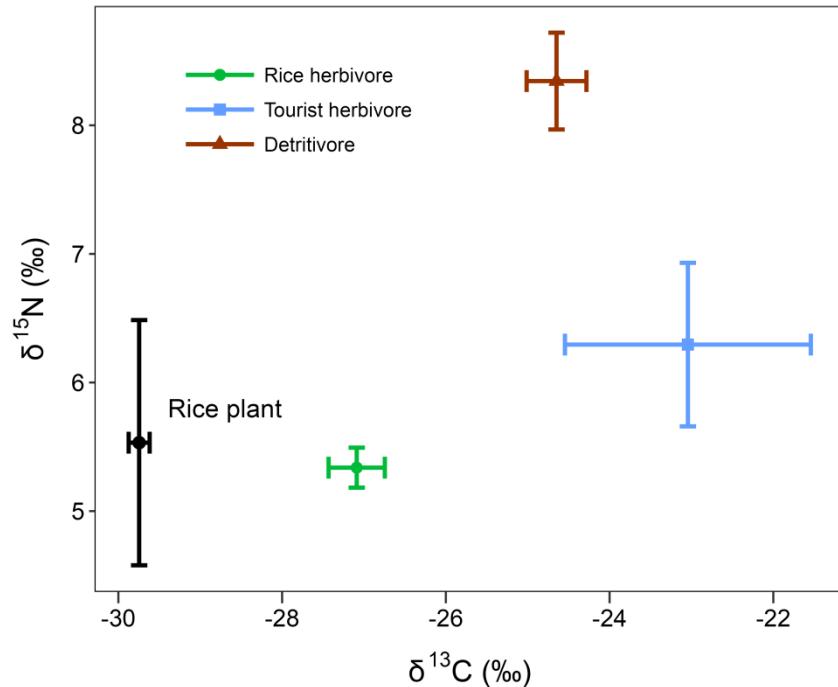
Family/Genus	Year 2017	Year 2018	Year 2019
Cicadellidae/ <i>Nephrotettix</i>	7.6%	22.5%	69.7%
Delphacidae/ <i>Nilaparvata</i>	88.2%	71.9%	25.4%
Lygaeidae/ <i>Pachybrachius</i>	NA	0.8%	1.3%
Pentatomidae/ <i>Scotinophara</i>	0.8%	2.9%	0.8%
Others	3.4%	1.9%	2.8%
<i>Total</i>	100%	100%	100%

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36 (b) Ripening stage

Family/Genus	Year 2017	Year 2018	Year 2019
Cicadellidae/ <i>Nephrotettix</i>	69.4%	74.9%	83.5%
Delphacidae/ <i>Nilaparvata</i>	28.9%	13.4%	6.2%
Lygaeidae/ <i>Pachybrachius</i>	NA	0.2%	4.1%
Pentatomidae/ <i>Scotinophara</i>	1.7%	10.4%	4.5%
Others	NA	1.1%	1.7%
<i>Total</i>	100%	100%	100%

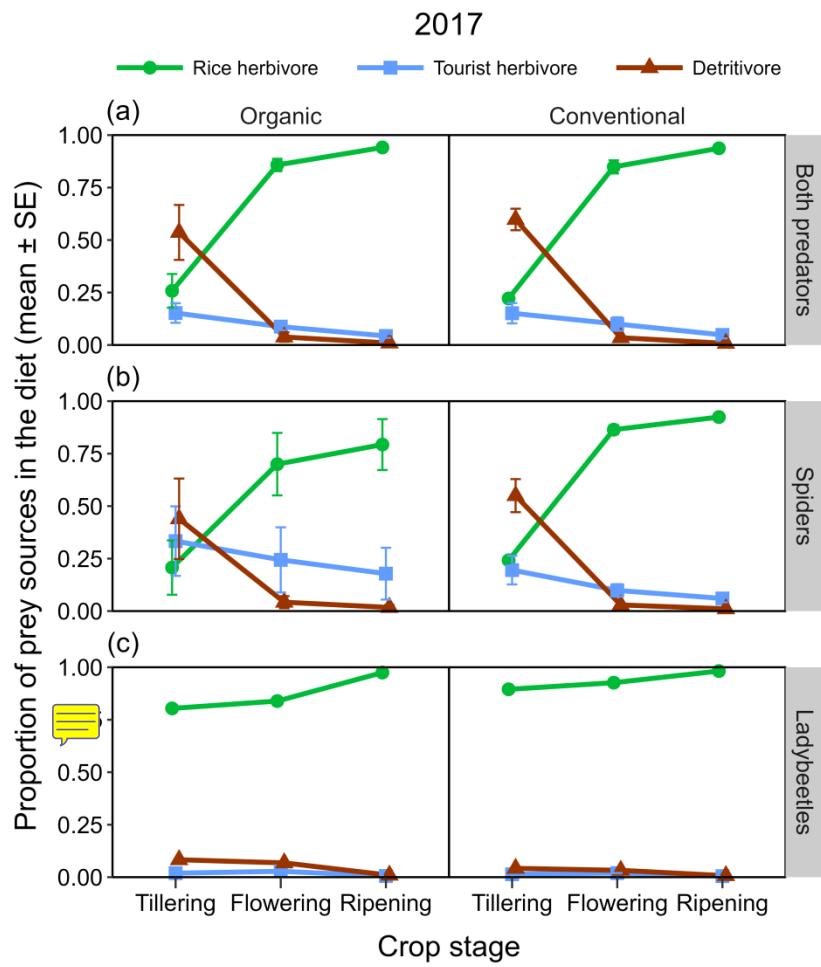
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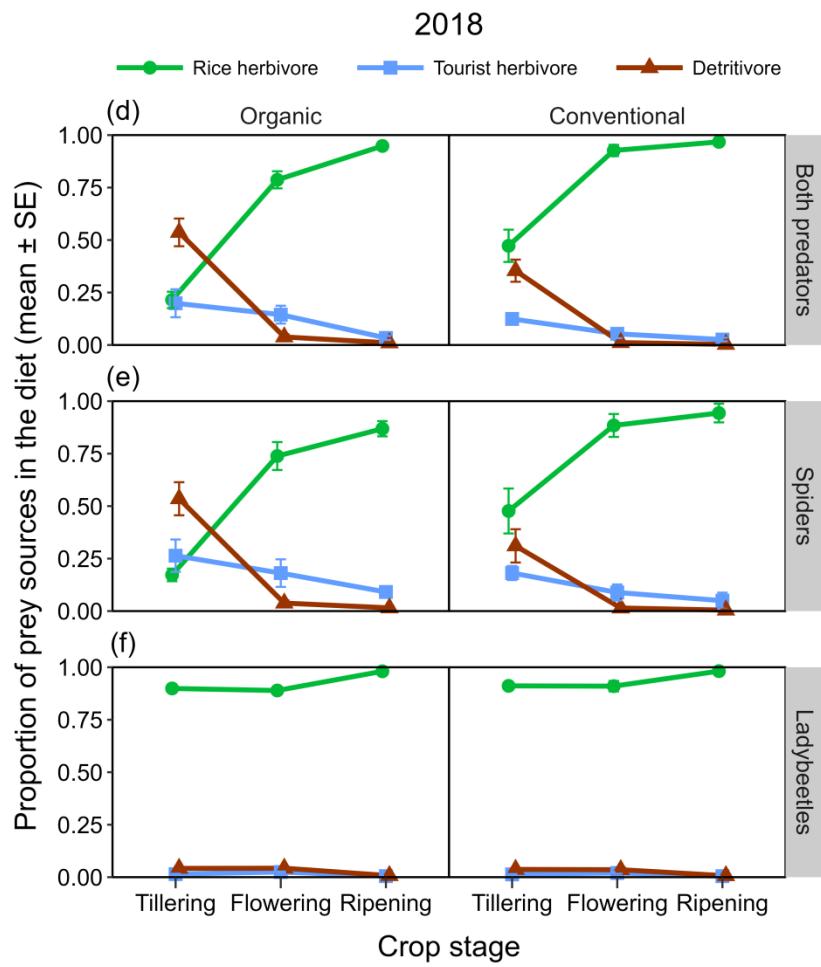
39  **Figure S1.** Stable isotope biplot of the rice plant and three prey sources in this study. Error bars
40 represent 95% confidence intervals.

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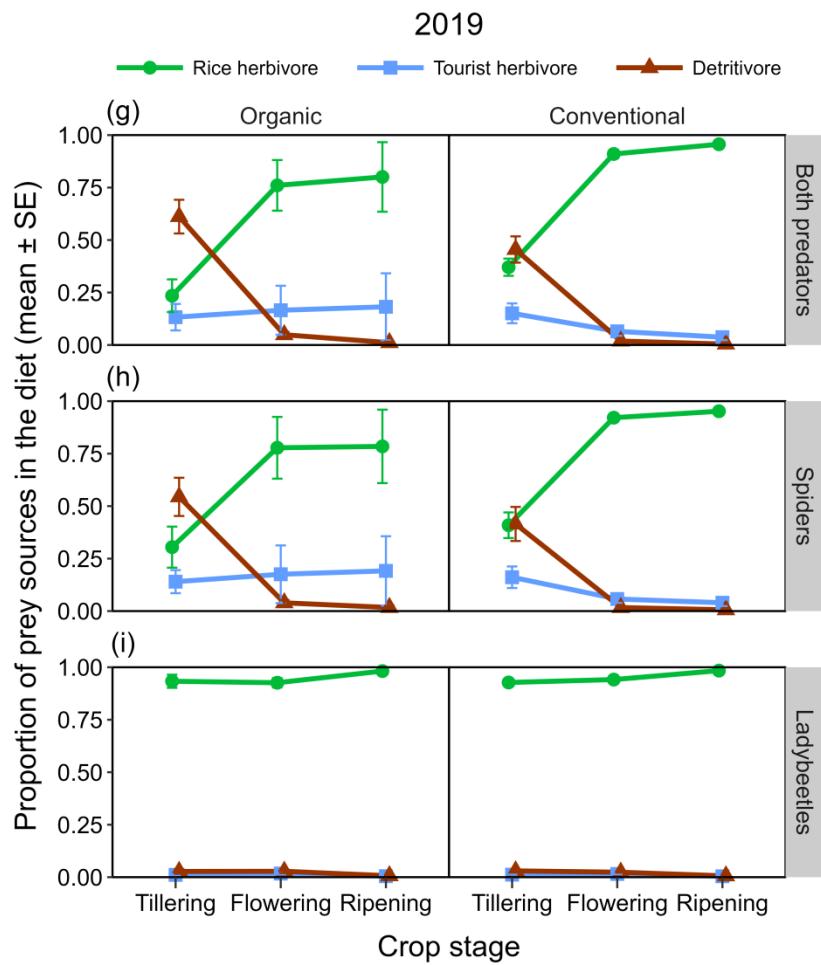
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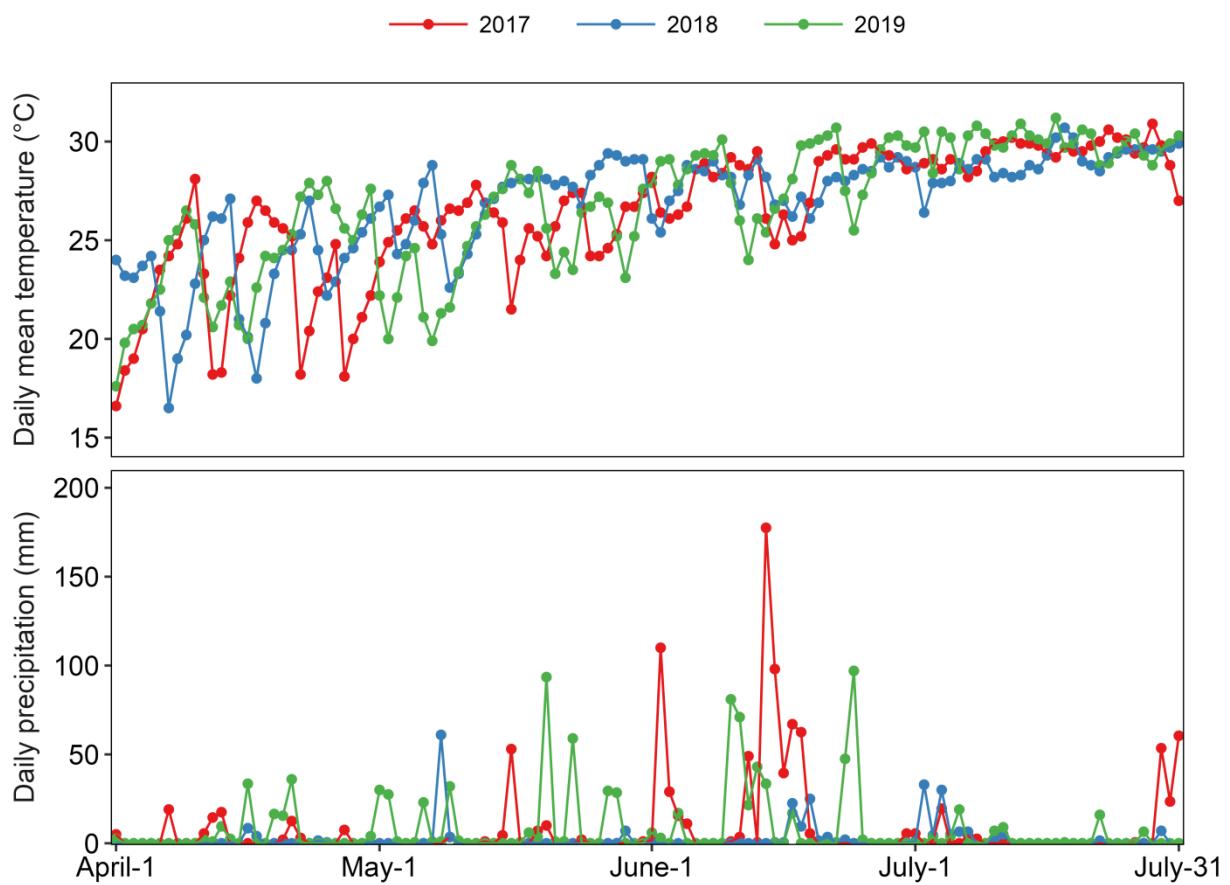
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48 **Figure S2.** proportions (mean \pm SE) of prey sources (rice herbivores, tourist herbivores, 49
detritivores) consumed in the diet of predators in organic and conventional rice farms over crop 50
stages in each study year: (a), (d), and (g) indicate both predators (spiders and ladybeetles) as a 51
whole feeding guild; (b), (e), and (h) indicate spiders; (c), (f), and (i) indicate ladybeetles. The 52
proportions were computed from the Bayesian posterior medians of diet estimates in replicate 53
farms.

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56 **Figure S3.** Daily mean temperature and precipitation of the study sites during the rice growth
 57 season (April to July) of the three study years. Observation data from the closest local weather
 58 station (Yuanli station) to the study farms were retrieved from the Central Weather Bureau
 59 Observation Data Inquire System (<https://e-service.cwb.gov.tw/HistoryDataQuery/index.jsp>).

Year	Predator	Farm_ID	Stage	Source	Mean	SD	Median	Lower 95%	Upper 95%
								credible interval limit	credible interval limit
2017	Both	LC1	Tillering	Rice herbivore	0.263	0.068	0.258	0.149	0.418
2017	Both	LC1	Tillering	Tourist herbivore	0.172	0.104	0.145	0.038	0.406
2017	Both	LC1	Tillering	Detritivore	0.564	0.133	0.581	0.299	0.781
2017	Both	LC1	Flowering	Rice herbivore	0.871	0.057	0.879	0.736	0.956
2017	Both	LC1	Flowering	Tourist herbivore	0.097	0.055	0.084	0.026	0.229
2017	Both	LC1	Flowering	Detritivore	0.032	0.02	0.028	0.007	0.085
2017	Both	LC1	Ripening	Rice herbivore	0.945	0.028	0.95	0.879	0.984
2017	Both	LC1	Ripening	Tourist herbivore	0.045	0.025	0.039	0.012	0.109
2017	Both	LC1	Ripening	Detritivore	0.009	0.009	0.006	0.001	0.036
2017	Both	LO1	Tillering	Rice herbivore	0.408	0.166	0.397	0.123	0.758
2017	Both	LO1	Tillering	Tourist herbivore	0.196	0.136	0.174	0.012	0.494
2017	Both	LO1	Tillering	Detritivore	0.396	0.208	0.372	0.067	0.829
2017	Both	LO1	Flowering	Rice herbivore	0.9	0.065	0.913	0.745	0.985
2017	Both	LO1	Flowering	Tourist herbivore	0.081	0.062	0.065	0.006	0.227
2017	Both	LO1	Flowering	Detritivore	0.02	0.022	0.012	0.001	0.088
2017	Both	LO1	Ripening	Rice herbivore	0.956	0.033	0.964	0.87	0.996
2017	Both	LO1	Ripening	Tourist herbivore	0.038	0.032	0.03	0.003	0.122
2017	Both	LO1	Ripening	Detritivore	0.006	0.009	0.003	0	0.029
2017	Both	MC1	Tillering	Rice herbivore	0.221	0.128	0.199	0.036	0.513
2017	Both	MC1	Tillering	Tourist herbivore	0.253	0.155	0.238	0.018	0.598
2017	Both	MC1	Tillering	Detritivore	0.526	0.2	0.519	0.154	0.915
2017	Both	MC1	Flowering	Rice herbivore	0.771	0.127	0.786	0.478	0.962
2017	Both	MC1	Flowering	Tourist herbivore	0.18	0.117	0.162	0.017	0.467
2017	Both	MC1	Flowering	Detritivore	0.049	0.055	0.03	0.003	0.214
2017	Both	MC1	Ripening	Rice herbivore	0.883	0.086	0.905	0.671	0.988
2017	Both	MC1	Ripening	Tourist herbivore	0.1	0.08	0.08	0.008	0.304
2017	Both	MC1	Ripening	Detritivore	0.017	0.029	0.007	0	0.104
2017	Both	MO1	Tillering	Rice herbivore	0.281	0.173	0.258	0.035	0.652
2017	Both	MO1	Tillering	Tourist herbivore	0.274	0.209	0.22	0.016	0.766
2017	Both	MO1	Tillering	Detritivore	0.445	0.194	0.442	0.094	0.824
2017	Both	MO1	Flowering	Rice herbivore	0.767	0.206	0.848	0.302	0.984
2017	Both	MO1	Flowering	Tourist herbivore	0.203	0.197	0.12	0.006	0.656
2017	Both	MO1	Flowering	Detritivore	0.03	0.033	0.019	0.002	0.119
2017	Both	MO1	Ripening	Rice herbivore	0.88	0.126	0.93	0.545	0.994
2017	Both	MO1	Ripening	Tourist herbivore	0.11	0.122	0.06	0.003	0.442
2017	Both	MO1	Ripening	Detritivore	0.01	0.015	0.005	0	0.051
2017	Both	SC1	Tillering	Rice herbivore	0.219	0.115	0.208	0.043	0.47
2017	Both	SC1	Tillering	Tourist herbivore	0.095	0.087	0.071	0.007	0.324
2017	Both	SC1	Tillering	Detritivore	0.685	0.146	0.694	0.37	0.933
2017	Both	SC1	Flowering	Rice herbivore	0.862	0.089	0.881	0.636	0.976

2017	Both	SC1	Flowering	Tourist herbivore	0.075	0.068	0.054	0.006	0.245
2017	Both	SC1	Flowering	Detritivore	0.063	0.056	0.046	0.008	0.216
2017	Both	SC1	Ripening	Rice herbivore	0.943	0.049	0.956	0.809	0.994
2017	Both	SC1	Ripening	Tourist herbivore	0.037	0.038	0.025	0.002	0.142
2017	Both	SC1	Ripening	Detritivore	0.02	0.029	0.01	0.001	0.102
2017	Both	SO1	Tillering	Rice herbivore	0.133	0.083	0.119	0.018	0.331
2017	Both	SO1	Tillering	Tourist herbivore	0.086	0.078	0.063	0.006	0.284
2017	Both	SO1	Tillering	Detritivore	0.781	0.12	0.795	0.522	0.962
2017	Both	SO1	Flowering	Rice herbivore	0.784	0.134	0.812	0.46	0.959
2017	Both	SO1	Flowering	Tourist herbivore	0.103	0.087	0.077	0.008	0.328
2017	Both	SO1	Flowering	Detritivore	0.114	0.1	0.083	0.014	0.404
2017	Both	SO1	Ripening	Rice herbivore	0.911	0.067	0.929	0.747	0.989
2017	Both	SO1	Ripening	Tourist herbivore	0.053	0.048	0.039	0.004	0.179
2017	Both	SO1	Ripening	Detritivore	0.036	0.043	0.02	0.002	0.159
2017	Spider	LC1	Tillering	Rice herbivore	0.248	0.05	0.245	0.163	0.356
2017	Spider	LC1	Tillering	Tourist herbivore	0.283	0.074	0.288	0.116	0.417
2017	Spider	LC1	Tillering	Detritivore	0.469	0.091	0.46	0.316	0.685
2017	Spider	LC1	Flowering	Rice herbivore	0.829	0.05	0.832	0.721	0.916
2017	Spider	LC1	Flowering	Tourist herbivore	0.145	0.047	0.142	0.066	0.247
2017	Spider	LC1	Flowering	Detritivore	0.026	0.018	0.022	0.005	0.071
2017	Spider	LC1	Ripening	Rice herbivore	0.897	0.039	0.902	0.806	0.961
2017	Spider	LC1	Ripening	Tourist herbivore	0.091	0.037	0.087	0.032	0.177
2017	Spider	LC1	Ripening	Detritivore	0.012	0.013	0.008	0.001	0.048
2017	Spider	LO1	Tillering	Rice herbivore	0.464	0.127	0.466	0.215	0.71
2017	Spider	LO1	Tillering	Tourist herbivore	0.28	0.107	0.283	0.055	0.486
2017	Spider	LO1	Tillering	Detritivore	0.256	0.157	0.223	0.046	0.662
2017	Spider	LO1	Flowering	Rice herbivore	0.905	0.04	0.909	0.816	0.969
2017	Spider	LO1	Flowering	Tourist herbivore	0.086	0.039	0.082	0.022	0.172
2017	Spider	LO1	Flowering	Detritivore	0.009	0.01	0.006	0.001	0.04
2017	Spider	LO1	Ripening	Rice herbivore	0.943	0.03	0.948	0.872	0.986
2017	Spider	LO1	Ripening	Tourist herbivore	0.052	0.029	0.048	0.01	0.122
2017	Spider	LO1	Ripening	Detritivore	0.004	0.007	0.002	0	0.023
2017	Spider	MC1	Tillering	Rice herbivore	0.271	0.106	0.265	0.09	0.494
2017	Spider	MC1	Tillering	Tourist herbivore	0.24	0.111	0.236	0.043	0.474
2017	Spider	MC1	Tillering	Detritivore	0.488	0.171	0.483	0.169	0.836
2017	Spider	MC1	Flowering	Rice herbivore	0.85	0.061	0.856	0.712	0.949
2017	Spider	MC1	Flowering	Tourist herbivore	0.119	0.055	0.112	0.032	0.244
2017	Spider	MC1	Flowering	Detritivore	0.031	0.031	0.022	0.003	0.115
2017	Spider	MC1	Ripening	Rice herbivore	0.91	0.047	0.918	0.802	0.977
2017	Spider	MC1	Ripening	Tourist herbivore	0.075	0.041	0.068	0.016	0.173
2017	Spider	MC1	Ripening	Detritivore	0.015	0.022	0.008	0	0.078
2017	Spider	MO1	Tillering	Rice herbivore	0.074	0.042	0.065	0.019	0.175

2017	Spider	MO1	Tillering	Tourist herbivore	0.618	0.179	0.642	0.23	0.892
2017	Spider	MO1	Tillering	Detritivore	0.308	0.189	0.274	0.039	0.732
2017	Spider	MO1	Flowering	Rice herbivore	0.412	0.107	0.412	0.204	0.622
2017	Spider	MO1	Flowering	Tourist herbivore	0.556	0.104	0.554	0.358	0.761
2017	Spider	MO1	Flowering	Detritivore	0.032	0.034	0.022	0.002	0.117
2017	Spider	MO1	Ripening	Rice herbivore	0.551	0.116	0.554	0.316	0.767
2017	Spider	MO1	Ripening	Tourist herbivore	0.43	0.114	0.425	0.22	0.663
2017	Spider	MO1	Ripening	Detritivore	0.019	0.024	0.01	0.001	0.089
2017	Spider	SC1	Tillering	Rice herbivore	0.221	0.109	0.216	0.042	0.446
2017	Spider	SC1	Tillering	Tourist herbivore	0.073	0.051	0.062	0.01	0.202
2017	Spider	SC1	Tillering	Detritivore	0.705	0.125	0.707	0.457	0.924
2017	Spider	SC1	Flowering	Rice herbivore	0.885	0.077	0.905	0.687	0.975
2017	Spider	SC1	Flowering	Tourist herbivore	0.054	0.044	0.042	0.006	0.165
2017	Spider	SC1	Flowering	Detritivore	0.062	0.055	0.044	0.007	0.217
2017	Spider	SC1	Ripening	Rice herbivore	0.932	0.065	0.953	0.743	0.992
2017	Spider	SC1	Ripening	Tourist herbivore	0.034	0.033	0.025	0.003	0.123
2017	Spider	SC1	Ripening	Detritivore	0.033	0.05	0.016	0.001	0.181
2017	Spider	SO1	Tillering	Rice herbivore	0.105	0.066	0.091	0.018	0.27
2017	Spider	SO1	Tillering	Tourist herbivore	0.086	0.056	0.075	0.01	0.224
2017	Spider	SO1	Tillering	Detritivore	0.809	0.096	0.822	0.6	0.958
2017	Spider	SO1	Flowering	Rice herbivore	0.759	0.128	0.779	0.463	0.946
2017	Spider	SO1	Flowering	Tourist herbivore	0.112	0.074	0.096	0.015	0.286
2017	Spider	SO1	Flowering	Detritivore	0.13	0.103	0.099	0.015	0.408
2017	Spider	SO1	Ripening	Rice herbivore	0.86	0.09	0.878	0.645	0.977
2017	Spider	SO1	Ripening	Tourist herbivore	0.075	0.055	0.062	0.009	0.214
2017	Spider	SO1	Ripening	Detritivore	0.066	0.07	0.04	0.003	0.259
2017	adybeetl	LC1	Flowering	Rice herbivore	0.902	0.131	0.934	0.456	0.991
2017	adybeetl	LC1	Flowering	Tourist herbivore	0.054	0.124	0.02	0	0.498
2017	adybeetl	LC1	Flowering	Detritivore	0.045	0.041	0.033	0.001	0.151
2017	adybeetl	LC1	Ripening	Rice herbivore	0.955	0.137	0.984	0.498	0.998
2017	adybeetl	LC1	Ripening	Tourist herbivore	0.033	0.135	0.005	0	0.472
2017	adybeetl	LC1	Ripening	Detritivore	0.012	0.014	0.007	0	0.049
2017	adybeetl	LO1	Ripening	Rice herbivore	0.944	0.143	0.984	0.474	0.999
2017	adybeetl	LO1	Ripening	Tourist herbivore	0.038	0.138	0.004	0	0.518
2017	adybeetl	LO1	Ripening	Detritivore	0.018	0.032	0.006	0	0.11
2017	adybeetl	MC1	Tillering	Rice herbivore	0.803	0.228	0.895	0.139	0.998
2017	adybeetl	MC1	Tillering	Tourist herbivore	0.08	0.165	0.014	0	0.657
2017	adybeetl	MC1	Tillering	Detritivore	0.118	0.165	0.042	0	0.605
2017	adybeetl	MO1	Tillering	Rice herbivore	0.74	0.239	0.804	0.153	0.998
2017	adybeetl	MO1	Tillering	Tourist herbivore	0.086	0.162	0.019	0	0.622
2017	adybeetl	MO1	Tillering	Detritivore	0.173	0.198	0.083	0	0.656
2017	adybeetl	MO1	Flowering	Rice herbivore	0.792	0.188	0.839	0.311	0.996

2017	adybeetl	MO1	Flowering	Tourist herbivore	0.085	0.141	0.028	0	0.53
2017	adybeetl	MO1	Flowering	Detritivore	0.123	0.138	0.068	0.001	0.484
2017	adybeetl	MO1	Ripening	Rice herbivore	0.914	0.141	0.959	0.515	0.999
2017	adybeetl	MO1	Ripening	Tourist herbivore	0.046	0.128	0.008	0	0.442
2017	adybeetl	MO1	Ripening	Detritivore	0.04	0.059	0.015	0	0.222
2017	adybeetl	SC1	Flowering	Rice herbivore	0.863	0.16	0.919	0.407	0.997
2017	adybeetl	SC1	Flowering	Tourist herbivore	0.069	0.133	0.019	0	0.5
2017	adybeetl	SC1	Flowering	Detritivore	0.068	0.091	0.032	0.001	0.324
2017	adybeetl	SC1	Ripening	Rice herbivore	0.94	0.138	0.98	0.565	0.999
2017	adybeetl	SC1	Ripening	Tourist herbivore	0.039	0.131	0.005	0	0.394
2017	adybeetl	SC1	Ripening	Detritivore	0.022	0.039	0.007	0	0.136
2017	adybeetl	SO1	Ripening	Rice herbivore	0.938	0.143	0.981	0.521	0.999
2017	adybeetl	SO1	Ripening	Tourist herbivore	0.039	0.134	0.005	0	0.477
2017	adybeetl	SO1	Ripening	Detritivore	0.023	0.044	0.007	0	0.165
2018	Both	LC1	Tillering	Rice herbivore	0.389	0.194	0.383	0.053	0.773
2018	Both	LC1	Tillering	Tourist herbivore	0.178	0.168	0.117	0.008	0.594
2018	Both	LC1	Tillering	Detritivore	0.432	0.225	0.398	0.077	0.911
2018	Both	LC1	Flowering	Rice herbivore	0.883	0.114	0.923	0.559	0.991
2018	Both	LC1	Flowering	Tourist herbivore	0.087	0.1	0.049	0.004	0.38
2018	Both	LC1	Flowering	Detritivore	0.03	0.053	0.013	0.001	0.183
2018	Both	LC1	Ripening	Rice herbivore	0.952	0.049	0.969	0.826	0.997
2018	Both	LC1	Ripening	Tourist herbivore	0.04	0.046	0.024	0.002	0.161
2018	Both	LC1	Ripening	Detritivore	0.008	0.013	0.003	0	0.045
2018	Both	LC2	Tillering	Rice herbivore	0.309	0.174	0.288	0.045	0.694
2018	Both	LC2	Tillering	Tourist herbivore	0.174	0.144	0.139	0.009	0.544
2018	Both	LC2	Tillering	Detritivore	0.517	0.213	0.524	0.107	0.902
2018	Both	LC2	Ripening	Rice herbivore	0.932	0.073	0.956	0.732	0.995
2018	Both	LC2	Ripening	Tourist herbivore	0.056	0.067	0.033	0.002	0.244
2018	Both	LC2	Ripening	Detritivore	0.012	0.021	0.005	0	0.071
2018	Both	LC3	Tillering	Rice herbivore	0.669	0.108	0.671	0.445	0.876
2018	Both	LC3	Tillering	Tourist herbivore	0.09	0.075	0.069	0.007	0.281
2018	Both	LC3	Tillering	Detritivore	0.241	0.11	0.234	0.057	0.475
2018	Both	LC3	Flowering	Rice herbivore	0.969	0.028	0.977	0.901	0.995
2018	Both	LC3	Flowering	Tourist herbivore	0.025	0.027	0.016	0.002	0.092
2018	Both	LC3	Flowering	Detritivore	0.006	0.006	0.005	0.001	0.022
2018	Both	LC3	Ripening	Rice herbivore	0.987	0.012	0.991	0.955	0.999
2018	Both	LC3	Ripening	Tourist herbivore	0.011	0.012	0.007	0.001	0.042
2018	Both	LC3	Ripening	Detritivore	0.002	0.002	0.001	0	0.008
2018	Both	LO1	Tillering	Rice herbivore	0.315	0.136	0.31	0.058	0.59
2018	Both	LO1	Tillering	Tourist herbivore	0.283	0.152	0.277	0.023	0.593
2018	Both	LO1	Tillering	Detritivore	0.402	0.172	0.387	0.106	0.79
2018	Both	LO1	Flowering	Rice herbivore	0.817	0.139	0.851	0.431	0.976

2018	Both	LO1	Flowering	Tourist herbivore	0.159	0.132	0.126	0.012	0.527
2018	Both	LO1	Flowering	Detritivore	0.024	0.029	0.015	0.002	0.104
2018	Both	LO1	Ripening	Rice herbivore	0.905	0.103	0.936	0.584	0.991
2018	Both	LO1	Ripening	Tourist herbivore	0.088	0.1	0.057	0.005	0.399
2018	Both	LO1	Ripening	Detritivore	0.007	0.011	0.004	0	0.037
2018	Both	LO2	Tillering	Rice herbivore	0.295	0.143	0.288	0.058	0.606
2018	Both	LO2	Tillering	Tourist herbivore	0.139	0.13	0.097	0.007	0.489
2018	Both	LO2	Tillering	Detritivore	0.565	0.187	0.567	0.184	0.896
2018	Both	LO2	Flowering	Rice herbivore	0.877	0.096	0.906	0.611	0.982
2018	Both	LO2	Flowering	Tourist herbivore	0.082	0.083	0.055	0.005	0.31
2018	Both	LO2	Flowering	Detritivore	0.04	0.045	0.026	0.004	0.169
2018	Both	LO2	Ripening	Rice herbivore	0.949	0.047	0.964	0.817	0.995
2018	Both	LO2	Ripening	Tourist herbivore	0.039	0.042	0.025	0.002	0.159
2018	Both	LO2	Ripening	Detritivore	0.012	0.017	0.006	0	0.058
2018	Both	LO3	Tillering	Rice herbivore	0.364	0.174	0.365	0.06	0.706
2018	Both	LO3	Tillering	Tourist herbivore	0.101	0.145	0.046	0.005	0.568
2018	Both	LO3	Tillering	Detritivore	0.536	0.198	0.527	0.143	0.906
2018	Both	LO3	Ripening	Rice herbivore	0.966	0.043	0.981	0.838	0.998
2018	Both	LO3	Ripening	Tourist herbivore	0.025	0.04	0.011	0.001	0.144
2018	Both	LO3	Ripening	Detritivore	0.01	0.015	0.005	0	0.049
2018	Both	MC1	Tillering	Rice herbivore	0.691	0.168	0.722	0.276	0.926
2018	Both	MC1	Tillering	Tourist herbivore	0.075	0.073	0.056	0.006	0.255
2018	Both	MC1	Tillering	Detritivore	0.234	0.171	0.188	0.027	0.659
2018	Both	MC1	Flowering	Rice herbivore	0.971	0.034	0.98	0.897	0.997
2018	Both	MC1	Flowering	Tourist herbivore	0.022	0.031	0.013	0.001	0.087
2018	Both	MC1	Flowering	Detritivore	0.007	0.011	0.004	0	0.033
2018	Both	MC1	Ripening	Rice herbivore	0.988	0.02	0.992	0.956	0.999
2018	Both	MC1	Ripening	Tourist herbivore	0.01	0.018	0.006	0.001	0.04
2018	Both	MC1	Ripening	Detritivore	0.002	0.005	0.001	0	0.011
2018	Both	MC2	Tillering	Rice herbivore	0.599	0.217	0.646	0.108	0.908
2018	Both	MC2	Tillering	Tourist herbivore	0.114	0.107	0.083	0.007	0.408
2018	Both	MC2	Tillering	Detritivore	0.287	0.219	0.221	0.033	0.829
2018	Both	MC2	Flowering	Rice herbivore	0.944	0.072	0.966	0.752	0.996
2018	Both	MC2	Flowering	Tourist herbivore	0.042	0.062	0.024	0.002	0.199
2018	Both	MC2	Flowering	Detritivore	0.014	0.029	0.005	0	0.087
2018	Both	MC2	Ripening	Rice herbivore	0.976	0.039	0.987	0.874	0.999
2018	Both	MC2	Ripening	Tourist herbivore	0.02	0.033	0.01	0.001	0.108
2018	Both	MC2	Ripening	Detritivore	0.004	0.014	0.001	0	0.026
2018	Both	MC3	Tillering	Rice herbivore	0.233	0.139	0.214	0.031	0.547
2018	Both	MC3	Tillering	Tourist herbivore	0.248	0.159	0.235	0.014	0.591
2018	Both	MC3	Tillering	Detritivore	0.518	0.206	0.509	0.138	0.915
2018	Both	MC3	Flowering	Rice herbivore	0.773	0.15	0.807	0.417	0.971

2018	Both	MC3	Flowering	Tourist herbivore	0.178	0.134	0.148	0.011	0.506
2018	Both	MC3	Flowering	Detritivore	0.049	0.066	0.027	0.003	0.239
2018	Both	MC3	Ripening	Rice herbivore	0.886	0.099	0.915	0.625	0.99
2018	Both	MC3	Ripening	Tourist herbivore	0.098	0.09	0.07	0.006	0.334
2018	Both	MC3	Ripening	Detritivore	0.016	0.03	0.007	0	0.097
2018	Both	MO1	Tillering	Rice herbivore	0.225	0.207	0.165	0.007	0.72
2018	Both	MO1	Tillering	Tourist herbivore	0.172	0.177	0.109	0.005	0.659
2018	Both	MO1	Tillering	Detritivore	0.602	0.278	0.618	0.097	0.984
2018	Both	MO1	Flowering	Rice herbivore	0.719	0.226	0.788	0.246	0.985
2018	Both	MO1	Flowering	Tourist herbivore	0.148	0.145	0.101	0.006	0.554
2018	Both	MO1	Flowering	Detritivore	0.133	0.183	0.036	0.002	0.619
2018	Both	MO1	Ripening	Rice herbivore	0.872	0.119	0.913	0.573	0.994
2018	Both	MO1	Ripening	Tourist herbivore	0.087	0.094	0.055	0.003	0.352
2018	Both	MO1	Ripening	Detritivore	0.041	0.066	0.011	0	0.237
2018	Both	MO2	Tillering	Rice herbivore	0.161	0.115	0.135	0.023	0.431
2018	Both	MO2	Tillering	Tourist herbivore	0.452	0.241	0.507	0.007	0.831
2018	Both	MO2	Tillering	Detritivore	0.387	0.271	0.306	0.051	0.955
2018	Both	MO2	Flowering	Rice herbivore	0.629	0.188	0.656	0.215	0.921
2018	Both	MO2	Flowering	Tourist herbivore	0.322	0.201	0.296	0.019	0.754
2018	Both	MO2	Flowering	Detritivore	0.049	0.08	0.019	0.002	0.303
2018	Both	MO3	Tillering	Rice herbivore	0.157	0.112	0.132	0.02	0.429
2018	Both	MO3	Tillering	Tourist herbivore	0.324	0.199	0.324	0.012	0.726
2018	Both	MO3	Tillering	Detritivore	0.519	0.236	0.5	0.102	0.946
2018	Both	MO3	Flowering	Rice herbivore	0.661	0.181	0.68	0.247	0.939
2018	Both	MO3	Flowering	Tourist herbivore	0.272	0.175	0.247	0.022	0.691
2018	Both	MO3	Flowering	Detritivore	0.066	0.085	0.033	0.003	0.336
2018	Both	SC1	Tillering	Rice herbivore	0.385	0.162	0.384	0.091	0.709
2018	Both	SC1	Tillering	Tourist herbivore	0.191	0.129	0.17	0.013	0.486
2018	Both	SC1	Tillering	Detritivore	0.424	0.198	0.404	0.094	0.831
2018	Both	SC1	Flowering	Rice herbivore	0.884	0.088	0.907	0.651	0.986
2018	Both	SC1	Flowering	Tourist herbivore	0.091	0.078	0.07	0.006	0.298
2018	Both	SC1	Flowering	Detritivore	0.025	0.037	0.014	0.002	0.116
2018	Both	SC1	Ripening	Rice herbivore	0.948	0.046	0.963	0.819	0.996
2018	Both	SC1	Ripening	Tourist herbivore	0.045	0.043	0.031	0.003	0.168
2018	Both	SC1	Ripening	Detritivore	0.007	0.014	0.003	0	0.039
2018	Both	SO1	Tillering	Rice herbivore	0.121	0.069	0.108	0.027	0.287
2018	Both	SO1	Tillering	Tourist herbivore	0.041	0.035	0.032	0.004	0.132
2018	Both	SO1	Tillering	Detritivore	0.838	0.082	0.85	0.651	0.96
2018	Both	SO1	Flowering	Rice herbivore	0.822	0.097	0.84	0.586	0.957
2018	Both	SO1	Flowering	Tourist herbivore	0.058	0.052	0.042	0.005	0.189
2018	Both	SO1	Flowering	Detritivore	0.12	0.08	0.101	0.021	0.325
2018	Both	SO1	Ripening	Rice herbivore	0.932	0.054	0.947	0.793	0.991

2018	Both	SO1	Ripening	Tourist herbivore	0.03	0.03	0.02	0.002	0.111
2018	Both	SO1	Ripening	Detritivore	0.038	0.042	0.024	0.002	0.157
2018	Spider	LC1	Tillering	Rice herbivore	0.12	0.104	0.088	0.007	0.373
2018	Spider	LC1	Tillering	Tourist herbivore	0.262	0.152	0.247	0.027	0.607
2018	Spider	LC1	Tillering	Detritivore	0.618	0.194	0.617	0.227	0.953
2018	Spider	LC1	Flowering	Rice herbivore	0.606	0.222	0.642	0.163	0.927
2018	Spider	LC1	Flowering	Tourist herbivore	0.282	0.173	0.249	0.04	0.684
2018	Spider	LC1	Flowering	Detritivore	0.112	0.139	0.053	0.006	0.521
2018	Spider	LC2	Tillering	Rice herbivore	0.297	0.162	0.285	0.034	0.65
2018	Spider	LC2	Tillering	Tourist herbivore	0.205	0.134	0.182	0.025	0.541
2018	Spider	LC2	Tillering	Detritivore	0.498	0.207	0.499	0.111	0.884
2018	Spider	LC3	Tillering	Rice herbivore	0.717	0.101	0.72	0.516	0.907
2018	Spider	LC3	Tillering	Tourist herbivore	0.094	0.062	0.081	0.014	0.243
2018	Spider	LC3	Tillering	Detritivore	0.189	0.101	0.178	0.031	0.413
2018	Spider	LC3	Flowering	Rice herbivore	0.975	0.017	0.978	0.935	0.996
2018	Spider	LC3	Flowering	Tourist herbivore	0.02	0.016	0.016	0.002	0.06
2018	Spider	LC3	Flowering	Detritivore	0.004	0.005	0.003	0	0.016
2018	Spider	LO1	Tillering	Rice herbivore	0.191	0.107	0.173	0.039	0.443
2018	Spider	LO1	Tillering	Tourist herbivore	0.38	0.14	0.372	0.119	0.677
2018	Spider	LO1	Tillering	Detritivore	0.429	0.177	0.424	0.103	0.787
2018	Spider	LO1	Flowering	Rice herbivore	0.708	0.14	0.729	0.38	0.915
2018	Spider	LO1	Flowering	Tourist herbivore	0.256	0.127	0.236	0.07	0.551
2018	Spider	LO1	Flowering	Detritivore	0.036	0.043	0.024	0.002	0.144
2018	Spider	LO1	Ripening	Rice herbivore	0.806	0.116	0.83	0.522	0.956
2018	Spider	LO1	Ripening	Tourist herbivore	0.175	0.106	0.153	0.037	0.432
2018	Spider	LO1	Ripening	Detritivore	0.019	0.033	0.009	0	0.088
2018	Spider	LO2	Tillering	Rice herbivore	0.332	0.115	0.328	0.115	0.568
2018	Spider	LO2	Tillering	Tourist herbivore	0.204	0.096	0.199	0.034	0.411
2018	Spider	LO2	Tillering	Detritivore	0.464	0.16	0.455	0.174	0.8
2018	Spider	LO2	Flowering	Rice herbivore	0.887	0.055	0.896	0.755	0.968
2018	Spider	LO2	Flowering	Tourist herbivore	0.088	0.047	0.08	0.018	0.195
2018	Spider	LO2	Flowering	Detritivore	0.025	0.026	0.017	0.002	0.097
2018	Spider	LO2	Ripening	Rice herbivore	0.934	0.038	0.941	0.842	0.985
2018	Spider	LO2	Ripening	Tourist herbivore	0.054	0.033	0.048	0.009	0.137
2018	Spider	LO2	Ripening	Detritivore	0.012	0.016	0.006	0	0.055
2018	Spider	LO3	Tillering	Rice herbivore	0.215	0.112	0.201	0.04	0.458
2018	Spider	LO3	Tillering	Tourist herbivore	0.171	0.105	0.156	0.018	0.416
2018	Spider	LO3	Tillering	Detritivore	0.614	0.169	0.624	0.273	0.914
2018	Spider	LO3	Ripening	Rice herbivore	0.9	0.07	0.917	0.71	0.982
2018	Spider	LO3	Ripening	Tourist herbivore	0.072	0.051	0.06	0.01	0.2
2018	Spider	LO3	Ripening	Detritivore	0.029	0.043	0.013	0.001	0.159
2018	Spider	MC1	Tillering	Rice herbivore	0.757	0.099	0.764	0.549	0.929

2018	Spider	MC1	Tillering	Tourist herbivore	0.12	0.08	0.104	0.015	0.307
2018	Spider	MC1	Tillering	Detritivore	0.123	0.077	0.107	0.021	0.316
2018	Spider	MC1	Flowering	Rice herbivore	0.972	0.022	0.977	0.915	0.996
2018	Spider	MC1	Flowering	Tourist herbivore	0.025	0.022	0.02	0.003	0.081
2018	Spider	MC1	Flowering	Detritivore	0.003	0.003	0.002	0	0.011
2018	Spider	MC1	Ripening	Rice herbivore	0.984	0.015	0.988	0.946	0.998
2018	Spider	MC1	Ripening	Tourist herbivore	0.015	0.015	0.011	0.001	0.052
2018	Spider	MC1	Ripening	Detritivore	0.001	0.002	0.001	0	0.007
2018	Spider	MC2	Tillering	Rice herbivore	0.773	0.104	0.787	0.54	0.936
2018	Spider	MC2	Tillering	Tourist herbivore	0.111	0.075	0.096	0.014	0.288
2018	Spider	MC2	Tillering	Detritivore	0.116	0.088	0.095	0.018	0.347
2018	Spider	MC2	Flowering	Rice herbivore	0.974	0.021	0.98	0.92	0.996
2018	Spider	MC2	Flowering	Tourist herbivore	0.023	0.021	0.018	0.002	0.075
2018	Spider	MC2	Flowering	Detritivore	0.003	0.004	0.002	0	0.012
2018	Spider	MC3	Tillering	Rice herbivore	0.251	0.119	0.241	0.056	0.515
2018	Spider	MC3	Tillering	Tourist herbivore	0.283	0.123	0.279	0.057	0.541
2018	Spider	MC3	Tillering	Detritivore	0.465	0.181	0.457	0.137	0.839
2018	Spider	MC3	Flowering	Rice herbivore	0.808	0.098	0.824	0.564	0.947
2018	Spider	MC3	Flowering	Tourist herbivore	0.158	0.084	0.144	0.035	0.358
2018	Spider	MC3	Flowering	Detritivore	0.035	0.042	0.022	0.002	0.153
2018	Spider	MC3	Ripening	Rice herbivore	0.881	0.073	0.899	0.695	0.975
2018	Spider	MC3	Ripening	Tourist herbivore	0.102	0.065	0.088	0.018	0.257
2018	Spider	MC3	Ripening	Detritivore	0.017	0.028	0.008	0	0.096
2018	Spider	MO1	Tillering	Rice herbivore	0.167	0.194	0.072	0.004	0.655
2018	Spider	MO1	Tillering	Tourist herbivore	0.181	0.185	0.109	0.006	0.658
2018	Spider	MO1	Tillering	Detritivore	0.652	0.306	0.754	0.086	0.987
2018	Spider	MO1	Flowering	Rice herbivore	0.607	0.26	0.61	0.188	0.974
2018	Spider	MO1	Flowering	Tourist herbivore	0.166	0.126	0.138	0.016	0.501
2018	Spider	MO1	Flowering	Detritivore	0.227	0.246	0.074	0.001	0.709
2018	Spider	MO1	Ripening	Rice herbivore	0.746	0.2	0.787	0.272	0.985
2018	Spider	MO1	Ripening	Tourist herbivore	0.129	0.106	0.103	0.009	0.388
2018	Spider	MO1	Ripening	Detritivore	0.125	0.175	0.033	0	0.612
2018	Spider	MO2	Tillering	Rice herbivore	0.147	0.078	0.135	0.03	0.33
2018	Spider	MO2	Tillering	Tourist herbivore	0.649	0.119	0.649	0.424	0.877
2018	Spider	MO2	Tillering	Detritivore	0.204	0.115	0.19	0.032	0.455
2018	Spider	MO2	Flowering	Rice herbivore	0.558	0.156	0.576	0.203	0.81
2018	Spider	MO2	Flowering	Tourist herbivore	0.427	0.153	0.409	0.182	0.767
2018	Spider	MO2	Flowering	Detritivore	0.016	0.018	0.01	0.001	0.06
2018	Spider	MO3	Tillering	Rice herbivore	0.165	0.107	0.147	0.019	0.419
2018	Spider	MO3	Tillering	Tourist herbivore	0.327	0.153	0.316	0.052	0.663
2018	Spider	MO3	Tillering	Detritivore	0.509	0.189	0.506	0.152	0.877
2018	Spider	SC1	Tillering	Rice herbivore	0.439	0.155	0.453	0.102	0.715

2018	Spider	SC1	Tillering	Tourist herbivore	0.287	0.125	0.281	0.066	0.554
2018	Spider	SC1	Tillering	Detritivore	0.274	0.19	0.222	0.041	0.773
2018	Spider	SC1	Flowering	Rice herbivore	0.883	0.08	0.905	0.67	0.973
2018	Spider	SC1	Flowering	Tourist herbivore	0.103	0.071	0.085	0.02	0.281
2018	Spider	SC1	Flowering	Detritivore	0.014	0.03	0.006	0.001	0.089
2018	Spider	SO1	Tillering	Rice herbivore	0.162	0.077	0.15	0.046	0.337
2018	Spider	SO1	Tillering	Tourist herbivore	0.056	0.039	0.047	0.007	0.152
2018	Spider	SO1	Tillering	Detritivore	0.782	0.091	0.793	0.581	0.931
2018	Spider	SO1	Flowering	Rice herbivore	0.869	0.069	0.882	0.707	0.966
2018	Spider	SO1	Flowering	Tourist herbivore	0.051	0.037	0.042	0.007	0.144
2018	Spider	SO1	Flowering	Detritivore	0.079	0.055	0.065	0.013	0.215
2018	adybeetl	LC1	Tillering	Rice herbivore	0.859	0.191	0.931	0.189	0.998
2018	adybeetl	LC1	Tillering	Tourist herbivore	0.067	0.159	0.012	0	0.671
2018	adybeetl	LC1	Tillering	Detritivore	0.074	0.109	0.03	0	0.389
2018	adybeetl	LC1	Ripening	Rice herbivore	0.95	0.138	0.986	0.51	0.999
2018	adybeetl	LC1	Ripening	Tourist herbivore	0.036	0.135	0.004	0	0.476
2018	adybeetl	LC1	Ripening	Detritivore	0.014	0.024	0.005	0	0.083
2018	adybeetl	LC2	Ripening	Rice herbivore	0.936	0.147	0.982	0.457	0.999
2018	adybeetl	LC2	Ripening	Tourist herbivore	0.042	0.139	0.005	0	0.501
2018	adybeetl	LC2	Ripening	Detritivore	0.023	0.045	0.006	0	0.152
2018	adybeetl	LC3	Tillering	Rice herbivore	0.854	0.187	0.924	0.197	0.998
2018	adybeetl	LC3	Tillering	Tourist herbivore	0.066	0.152	0.013	0	0.604
2018	adybeetl	LC3	Tillering	Detritivore	0.081	0.112	0.032	0	0.405
2018	adybeetl	LC3	Flowering	Rice herbivore	0.888	0.148	0.935	0.421	0.997
2018	adybeetl	LC3	Flowering	Tourist herbivore	0.06	0.129	0.016	0	0.51
2018	adybeetl	LC3	Flowering	Detritivore	0.052	0.069	0.026	0.001	0.253
2018	adybeetl	LC3	Ripening	Rice herbivore	0.948	0.14	0.985	0.388	0.999
2018	adybeetl	LC3	Ripening	Tourist herbivore	0.037	0.136	0.004	0	0.588
2018	adybeetl	LC3	Ripening	Detritivore	0.015	0.026	0.006	0	0.087
2018	adybeetl	LO1	Tillering	Rice herbivore	0.77	0.216	0.825	0.21	0.998
2018	adybeetl	LO1	Tillering	Tourist herbivore	0.094	0.162	0.021	0	0.589
2018	adybeetl	LO1	Tillering	Detritivore	0.135	0.159	0.07	0	0.543
2018	adybeetl	LO1	Flowering	Rice herbivore	0.816	0.18	0.869	0.322	0.995
2018	adybeetl	LO1	Flowering	Tourist herbivore	0.091	0.149	0.029	0	0.578
2018	adybeetl	LO1	Flowering	Detritivore	0.093	0.111	0.053	0.001	0.411
2018	adybeetl	LO1	Ripening	Rice herbivore	0.92	0.153	0.968	0.347	0.999
2018	adybeetl	LO1	Ripening	Tourist herbivore	0.052	0.145	0.008	0	0.611
2018	adybeetl	LO1	Ripening	Detritivore	0.028	0.046	0.012	0	0.154
2018	adybeetl	LO2	Tillering	Rice herbivore	0.827	0.228	0.925	0.11	0.998
2018	adybeetl	LO2	Tillering	Tourist herbivore	0.07	0.17	0.013	0	0.782
2018	adybeetl	LO2	Tillering	Detritivore	0.103	0.163	0.031	0	0.591
2018	adybeetl	LO2	Ripening	Rice herbivore	0.94	0.144	0.983	0.497	0.999

2018	adybeetl	LO2	Ripening	Tourist herbivore	0.039	0.137	0.004	0	0.461
2018	adybeetl	LO2	Ripening	Detritivore	0.021	0.041	0.006	0	0.136
2018	adybeetl	LO3	Tillering	Rice herbivore	0.831	0.212	0.915	0.115	0.998
2018	adybeetl	LO3	Tillering	Tourist herbivore	0.063	0.159	0.012	0	0.681
2018	adybeetl	LO3	Tillering	Detritivore	0.106	0.148	0.038	0	0.524
2018	adybeetl	LO3	Ripening	Rice herbivore	0.944	0.144	0.983	0.437	0.999
2018	adybeetl	LO3	Ripening	Tourist herbivore	0.036	0.138	0.004	0	0.533
2018	adybeetl	LO3	Ripening	Detritivore	0.02	0.034	0.007	0	0.116
2018	adybeetl	MC1	Tillering	Rice herbivore	0.829	0.223	0.921	0.127	0.998
2018	adybeetl	MC1	Tillering	Tourist herbivore	0.068	0.166	0.012	0	0.767
2018	adybeetl	MC1	Tillering	Detritivore	0.102	0.157	0.034	0	0.596
2018	adybeetl	MC2	Ripening	Rice herbivore	0.932	0.147	0.981	0.474	0.999
2018	adybeetl	MC2	Ripening	Tourist herbivore	0.043	0.134	0.005	0	0.465
2018	adybeetl	MC2	Ripening	Detritivore	0.025	0.054	0.007	0	0.169
2018	adybeetl	MO1	Ripening	Rice herbivore	0.935	0.145	0.981	0.465	0.999
2018	adybeetl	MO1	Ripening	Tourist herbivore	0.042	0.136	0.005	0	0.486
2018	adybeetl	MO1	Ripening	Detritivore	0.023	0.046	0.007	0	0.163
2018	adybeetl	MO2	Tillering	Rice herbivore	0.806	0.231	0.903	0.1	0.998
2018	adybeetl	MO2	Tillering	Tourist herbivore	0.084	0.176	0.015	0	0.719
2018	adybeetl	MO2	Tillering	Detritivore	0.11	0.161	0.041	0	0.609
2018	adybeetl	MO2	Flowering	Rice herbivore	0.847	0.185	0.914	0.262	0.997
2018	adybeetl	MO2	Flowering	Tourist herbivore	0.077	0.155	0.02	0	0.598
2018	adybeetl	MO2	Flowering	Detritivore	0.076	0.105	0.033	0.001	0.389
2018	adybeetl	MO3	Tillering	Rice herbivore	0.767	0.255	0.871	0.083	0.998
2018	adybeetl	MO3	Tillering	Tourist herbivore	0.1	0.188	0.017	0	0.75
2018	adybeetl	MO3	Tillering	Detritivore	0.133	0.188	0.051	0	0.697
2018	adybeetl	MO3	Flowering	Rice herbivore	0.806	0.209	0.885	0.209	0.996
2018	adybeetl	MO3	Flowering	Tourist herbivore	0.096	0.164	0.025	0	0.617
2018	adybeetl	MO3	Flowering	Detritivore	0.098	0.135	0.042	0.001	0.506
2018	adybeetl	SC1	Tillering	Rice herbivore	0.788	0.222	0.869	0.191	0.998
2018	adybeetl	SC1	Tillering	Tourist herbivore	0.08	0.156	0.017	0	0.614
2018	adybeetl	SC1	Tillering	Detritivore	0.131	0.17	0.052	0	0.613
2018	adybeetl	SC1	Flowering	Rice herbivore	0.834	0.168	0.885	0.384	0.996
2018	adybeetl	SC1	Flowering	Tourist herbivore	0.075	0.127	0.024	0	0.473
2018	adybeetl	SC1	Flowering	Detritivore	0.091	0.112	0.045	0.001	0.396
2018	adybeetl	SC1	Ripening	Rice herbivore	0.93	0.136	0.974	0.523	0.999
2018	adybeetl	SC1	Ripening	Tourist herbivore	0.042	0.126	0.006	0	0.413
2018	adybeetl	SC1	Ripening	Detritivore	0.028	0.043	0.01	0	0.16
2018	adybeetl	SO1	Tillering	Rice herbivore	0.865	0.235	0.955	0.064	0.998
2018	adybeetl	SO1	Tillering	Tourist herbivore	0.056	0.167	0.009	0	0.836
2018	adybeetl	SO1	Tillering	Detritivore	0.079	0.172	0.02	0	0.724
2018	adybeetl	SO1	Ripening	Rice herbivore	0.948	0.148	0.989	0.395	1

2018	adybeetl	SO1	Ripening	Tourist herbivore	0.035	0.14	0.003	0	0.483
2018	adybeetl	SO1	Ripening	Detritivore	0.017	0.044	0.004	0	0.148
2019	Both	LC1	Tillering	Rice herbivore	0.443	0.108	0.447	0.225	0.654
2019	Both	LC1	Tillering	Tourist herbivore	0.273	0.105	0.274	0.061	0.475
2019	Both	LC1	Tillering	Detritivore	0.284	0.136	0.267	0.076	0.61
2019	Both	LC1	Flowering	Rice herbivore	0.882	0.068	0.894	0.724	0.975
2019	Both	LC1	Flowering	Tourist herbivore	0.107	0.067	0.094	0.017	0.26
2019	Both	LC1	Flowering	Detritivore	0.011	0.013	0.008	0.001	0.045
2019	Both	LC1	Ripening	Rice herbivore	0.946	0.037	0.955	0.852	0.99
2019	Both	LC1	Ripening	Tourist herbivore	0.051	0.036	0.043	0.008	0.143
2019	Both	LC1	Ripening	Detritivore	0.003	0.004	0.002	0	0.014
2019	Both	LC2	Tillering	Rice herbivore	0.384	0.124	0.386	0.132	0.62
2019	Both	LC2	Tillering	Tourist herbivore	0.104	0.09	0.082	0.008	0.349
2019	Both	LC2	Tillering	Detritivore	0.511	0.142	0.511	0.226	0.801
2019	Both	LC2	Flowering	Rice herbivore	0.925	0.061	0.943	0.765	0.987
2019	Both	LC2	Flowering	Tourist herbivore	0.05	0.054	0.033	0.003	0.194
2019	Both	LC2	Flowering	Detritivore	0.025	0.023	0.019	0.004	0.089
2019	Both	LC3	Tillering	Rice herbivore	0.281	0.102	0.28	0.087	0.483
2019	Both	LC3	Tillering	Tourist herbivore	0.074	0.058	0.059	0.007	0.219
2019	Both	LC3	Tillering	Detritivore	0.645	0.116	0.645	0.42	0.878
2019	Both	LC3	Flowering	Rice herbivore	0.91	0.06	0.925	0.757	0.98
2019	Both	LC3	Flowering	Tourist herbivore	0.047	0.044	0.034	0.004	0.166
2019	Both	LC3	Flowering	Detritivore	0.042	0.036	0.032	0.007	0.139
2019	Both	LC3	Ripening	Rice herbivore	0.966	0.028	0.974	0.885	0.995
2019	Both	LC3	Ripening	Tourist herbivore	0.022	0.022	0.015	0.002	0.083
2019	Both	LC3	Ripening	Detritivore	0.012	0.015	0.007	0.001	0.051
2019	Both	LO1	Tillering	Rice herbivore	0.629	0.135	0.64	0.33	0.867
2019	Both	LO1	Tillering	Tourist herbivore	0.134	0.102	0.113	0.01	0.382
2019	Both	LO1	Tillering	Detritivore	0.237	0.133	0.216	0.042	0.545
2019	Both	LO1	Flowering	Rice herbivore	0.951	0.045	0.964	0.83	0.995
2019	Both	LO1	Flowering	Tourist herbivore	0.041	0.043	0.029	0.002	0.159
2019	Both	LO1	Flowering	Detritivore	0.007	0.01	0.004	0.001	0.03
2019	Both	LO1	Ripening	Rice herbivore	0.98	0.02	0.986	0.925	0.998
2019	Both	LO1	Ripening	Tourist herbivore	0.018	0.019	0.013	0.001	0.072
2019	Both	LO1	Ripening	Detritivore	0.002	0.003	0.001	0	0.009
2019	Both	LO2	Tillering	Rice herbivore	0.28	0.114	0.278	0.073	0.507
2019	Both	LO2	Tillering	Tourist herbivore	0.096	0.077	0.078	0.007	0.287
2019	Both	LO2	Tillering	Detritivore	0.623	0.131	0.621	0.37	0.875
2019	Both	LO2	Flowering	Rice herbivore	0.894	0.082	0.915	0.679	0.98
2019	Both	LO2	Flowering	Tourist herbivore	0.064	0.068	0.044	0.005	0.238
2019	Both	LO2	Flowering	Detritivore	0.042	0.038	0.031	0.007	0.147
2019	Both	LO3	Tillering	Rice herbivore	0.368	0.272	0.268	0.067	0.944

2019	Both	LO3	Tillering	Tourist herbivore	0.039	0.034	0.029	0.004	0.128
2019	Both	LO3	Tillering	Detritivore	0.593	0.278	0.69	0.026	0.911
2019	Both	LO3	Flowering	Rice herbivore	0.93	0.059	0.944	0.773	0.997
2019	Both	LO3	Flowering	Tourist herbivore	0.026	0.03	0.017	0.001	0.111
2019	Both	LO3	Flowering	Detritivore	0.044	0.044	0.033	0	0.16
2019	Both	LO3	Ripening	Rice herbivore	0.976	0.023	0.983	0.915	0.999
2019	Both	LO3	Ripening	Tourist herbivore	0.012	0.015	0.007	0.001	0.05
2019	Both	LO3	Ripening	Detritivore	0.011	0.014	0.007	0	0.05
2019	Both	MC1	Tillering	Rice herbivore	0.554	0.163	0.564	0.207	0.841
2019	Both	MC1	Tillering	Tourist herbivore	0.134	0.109	0.104	0.01	0.408
2019	Both	MC1	Tillering	Detritivore	0.311	0.169	0.283	0.055	0.707
2019	Both	MC1	Flowering	Rice herbivore	0.943	0.048	0.958	0.819	0.993
2019	Both	MC1	Flowering	Tourist herbivore	0.046	0.045	0.031	0.003	0.164
2019	Both	MC1	Flowering	Detritivore	0.011	0.014	0.007	0.001	0.05
2019	Both	MC1	Ripening	Rice herbivore	0.975	0.025	0.983	0.908	0.998
2019	Both	MC1	Ripening	Tourist herbivore	0.021	0.023	0.014	0.001	0.086
2019	Both	MC1	Ripening	Detritivore	0.003	0.005	0.002	0	0.018
2019	Both	MC2	Tillering	Rice herbivore	0.379	0.136	0.366	0.149	0.684
2019	Both	MC2	Tillering	Tourist herbivore	0.084	0.074	0.063	0.007	0.273
2019	Both	MC2	Tillering	Detritivore	0.537	0.156	0.548	0.189	0.805
2019	Both	MC2	Flowering	Rice herbivore	0.938	0.036	0.945	0.852	0.986
2019	Both	MC2	Flowering	Tourist herbivore	0.036	0.03	0.028	0.003	0.115
2019	Both	MC2	Flowering	Detritivore	0.026	0.019	0.021	0.004	0.077
2019	Both	MC3	Tillering	Rice herbivore	0.298	0.115	0.293	0.095	0.538
2019	Both	MC3	Tillering	Tourist herbivore	0.374	0.131	0.38	0.093	0.622
2019	Both	MC3	Tillering	Detritivore	0.328	0.161	0.305	0.077	0.707
2019	Both	MC3	Flowering	Rice herbivore	0.782	0.119	0.803	0.503	0.958
2019	Both	MC3	Flowering	Tourist herbivore	0.2	0.116	0.18	0.029	0.473
2019	Both	MC3	Flowering	Detritivore	0.018	0.02	0.012	0.002	0.077
2019	Both	MC3	Ripening	Rice herbivore	0.893	0.065	0.906	0.735	0.979
2019	Both	MC3	Ripening	Tourist herbivore	0.101	0.064	0.089	0.017	0.256
2019	Both	MC3	Ripening	Detritivore	0.005	0.008	0.003	0	0.026
2019	Both	MO1	Tillering	Rice herbivore	0.2	0.121	0.185	0.027	0.478
2019	Both	MO1	Tillering	Tourist herbivore	0.141	0.115	0.113	0.008	0.42
2019	Both	MO1	Tillering	Detritivore	0.659	0.177	0.674	0.245	0.949
2019	Both	MO1	Flowering	Rice herbivore	0.812	0.117	0.833	0.539	0.968
2019	Both	MO1	Flowering	Tourist herbivore	0.115	0.09	0.092	0.008	0.337
2019	Both	MO1	Flowering	Detritivore	0.072	0.081	0.046	0.006	0.303
2019	Both	MO1	Ripening	Rice herbivore	0.914	0.075	0.936	0.713	0.991
2019	Both	MO1	Ripening	Tourist herbivore	0.059	0.053	0.045	0.004	0.203
2019	Both	MO1	Ripening	Detritivore	0.027	0.049	0.01	0.001	0.175
2019	Both	MO2	Tillering	Rice herbivore	0.066	0.044	0.055	0.013	0.182

2019	Both	MO2	Tillering	Tourist herbivore	0.296	0.378	0.021	0.002	0.931
2019	Both	MO2	Tillering	Detritivore	0.639	0.387	0.901	0.025	0.974
2019	Both	MO2	Flowering	Rice herbivore	0.625	0.242	0.717	0.086	0.904
2019	Both	MO2	Flowering	Tourist herbivore	0.243	0.305	0.06	0.006	0.901
2019	Both	MO2	Flowering	Detritivore	0.132	0.113	0.122	0.002	0.371
2019	Both	MO3	Tillering	Rice herbivore	0.008	0.006	0.006	0.001	0.023
2019	Both	MO3	Tillering	Tourist herbivore	0.534	0.195	0.502	0.227	0.961
2019	Both	MO3	Tillering	Detritivore	0.458	0.195	0.492	0.033	0.766
2019	Both	MO3	Flowering	Rice herbivore	0.072	0.044	0.062	0.015	0.182
2019	Both	MO3	Flowering	Tourist herbivore	0.856	0.067	0.864	0.71	0.962
2019	Both	MO3	Flowering	Detritivore	0.072	0.048	0.063	0.006	0.19
2019	Both	MO3	Ripening	Rice herbivore	0.146	0.063	0.139	0.043	0.285
2019	Both	MO3	Ripening	Tourist herbivore	0.816	0.069	0.82	0.669	0.936
2019	Both	MO3	Ripening	Detritivore	0.038	0.036	0.028	0.002	0.135
2019	Both	SC1	Tillering	Rice herbivore	0.26	0.099	0.258	0.079	0.458
2019	Both	SC1	Tillering	Tourist herbivore	0.113	0.084	0.095	0.008	0.31
2019	Both	SC1	Tillering	Detritivore	0.627	0.124	0.626	0.384	0.865
2019	Both	SC1	Flowering	Rice herbivore	0.883	0.076	0.902	0.676	0.975
2019	Both	SC1	Flowering	Tourist herbivore	0.074	0.065	0.055	0.006	0.256
2019	Both	SC1	Flowering	Detritivore	0.043	0.034	0.032	0.007	0.136
2019	Both	SC1	Ripening	Rice herbivore	0.949	0.047	0.963	0.82	0.994
2019	Both	SC1	Ripening	Tourist herbivore	0.038	0.041	0.025	0.003	0.157
2019	Both	SC1	Ripening	Detritivore	0.013	0.018	0.007	0.001	0.06
2019	Both	SO1	Tillering	Rice herbivore	0.232	0.129	0.211	0.051	0.536
2019	Both	SO1	Tillering	Tourist herbivore	0.1	0.096	0.072	0.006	0.364
2019	Both	SO1	Tillering	Detritivore	0.667	0.165	0.687	0.301	0.921
2019	Both	SO1	Flowering	Rice herbivore	0.869	0.088	0.888	0.654	0.978
2019	Both	SO1	Flowering	Tourist herbivore	0.073	0.067	0.053	0.005	0.252
2019	Both	SO1	Flowering	Detritivore	0.059	0.053	0.043	0.006	0.198
2019	Both	SO1	Ripening	Rice herbivore	0.946	0.047	0.959	0.827	0.994
2019	Both	SO1	Ripening	Tourist herbivore	0.036	0.038	0.025	0.002	0.141
2019	Both	SO1	Ripening	Detritivore	0.018	0.025	0.009	0.001	0.085
2019	Spider	LC1	Tillering	Rice herbivore	0.502	0.084	0.505	0.33	0.655
2019	Spider	LC1	Tillering	Tourist herbivore	0.294	0.073	0.293	0.154	0.44
2019	Spider	LC1	Tillering	Detritivore	0.203	0.1	0.19	0.047	0.448
2019	Spider	LC1	Flowering	Rice herbivore	0.908	0.038	0.915	0.816	0.965
2019	Spider	LC1	Flowering	Tourist herbivore	0.085	0.037	0.079	0.031	0.173
2019	Spider	LC1	Flowering	Detritivore	0.007	0.007	0.005	0.001	0.024
2019	Spider	LC1	Ripening	Rice herbivore	0.945	0.027	0.951	0.878	0.982
2019	Spider	LC1	Ripening	Tourist herbivore	0.051	0.026	0.047	0.016	0.116
2019	Spider	LC1	Ripening	Detritivore	0.003	0.004	0.002	0	0.014
2019	Spider	LC2	Tillering	Rice herbivore	0.457	0.101	0.46	0.251	0.657

2019	Spider	LC2	Tillering	Tourist herbivore	0.127	0.068	0.117	0.024	0.284
2019	Spider	LC2	Tillering	Detritivore	0.416	0.122	0.411	0.191	0.67
2019	Spider	LC2	Flowering	Rice herbivore	0.942	0.032	0.948	0.865	0.985
2019	Spider	LC2	Flowering	Tourist herbivore	0.042	0.027	0.036	0.007	0.111
2019	Spider	LC2	Flowering	Detritivore	0.016	0.015	0.011	0.002	0.054
2019	Spider	LC3	Tillering	Rice herbivore	0.307	0.092	0.311	0.114	0.482
2019	Spider	LC3	Tillering	Tourist herbivore	0.05	0.031	0.044	0.008	0.126
2019	Spider	LC3	Tillering	Detritivore	0.643	0.099	0.638	0.452	0.848
2019	Spider	LC3	Flowering	Rice herbivore	0.939	0.038	0.947	0.838	0.984
2019	Spider	LC3	Flowering	Tourist herbivore	0.025	0.019	0.02	0.004	0.076
2019	Spider	LC3	Flowering	Detritivore	0.036	0.029	0.028	0.006	0.112
2019	Spider	LC3	Ripening	Rice herbivore	0.968	0.025	0.975	0.9	0.995
2019	Spider	LC3	Ripening	Tourist herbivore	0.015	0.013	0.012	0.002	0.048
2019	Spider	LC3	Ripening	Detritivore	0.016	0.019	0.01	0.001	0.072
2019	Spider	LO1	Tillering	Rice herbivore	0.74	0.089	0.744	0.556	0.9
2019	Spider	LO1	Tillering	Tourist herbivore	0.115	0.065	0.105	0.021	0.265
2019	Spider	LO1	Tillering	Detritivore	0.146	0.085	0.132	0.028	0.351
2019	Spider	LO1	Flowering	Rice herbivore	0.973	0.018	0.976	0.928	0.995
2019	Spider	LO1	Flowering	Tourist herbivore	0.024	0.017	0.02	0.003	0.068
2019	Spider	LO1	Flowering	Detritivore	0.003	0.003	0.002	0	0.012
2019	Spider	LO1	Ripening	Rice herbivore	0.984	0.011	0.987	0.955	0.998
2019	Spider	LO1	Ripening	Tourist herbivore	0.014	0.011	0.011	0.002	0.043
2019	Spider	LO1	Ripening	Detritivore	0.002	0.002	0.001	0	0.007
2019	Spider	LO2	Tillering	Rice herbivore	0.311	0.097	0.312	0.118	0.497
2019	Spider	LO2	Tillering	Tourist herbivore	0.066	0.041	0.059	0.011	0.166
2019	Spider	LO2	Tillering	Detritivore	0.623	0.11	0.621	0.413	0.843
2019	Spider	LO2	Flowering	Rice herbivore	0.932	0.04	0.942	0.825	0.982
2019	Spider	LO2	Flowering	Tourist herbivore	0.033	0.024	0.027	0.005	0.092
2019	Spider	LO2	Flowering	Detritivore	0.035	0.03	0.026	0.005	0.118
2019	Spider	LO3	Tillering	Rice herbivore	0.555	0.097	0.556	0.36	0.746
2019	Spider	LO3	Tillering	Tourist herbivore	0.126	0.07	0.117	0.02	0.288
2019	Spider	LO3	Tillering	Detritivore	0.319	0.116	0.316	0.102	0.56
2019	Spider	LO3	Flowering	Rice herbivore	0.956	0.024	0.961	0.896	0.988
2019	Spider	LO3	Flowering	Tourist herbivore	0.034	0.022	0.03	0.005	0.094
2019	Spider	LO3	Flowering	Detritivore	0.009	0.008	0.007	0.001	0.031
2019	Spider	LO3	Ripening	Rice herbivore	0.975	0.016	0.979	0.934	0.995
2019	Spider	LO3	Ripening	Tourist herbivore	0.02	0.015	0.017	0.003	0.058
2019	Spider	LO3	Ripening	Detritivore	0.004	0.005	0.003	0	0.02
2019	Spider	MC1	Tillering	Rice herbivore	0.704	0.109	0.707	0.474	0.899
2019	Spider	MC1	Tillering	Tourist herbivore	0.098	0.066	0.084	0.014	0.26
2019	Spider	MC1	Tillering	Detritivore	0.199	0.11	0.183	0.034	0.454
2019	Spider	MC1	Flowering	Rice herbivore	0.974	0.017	0.978	0.931	0.995

2019	Spider	MC1	Flowering	Tourist herbivore	0.021	0.017	0.017	0.003	0.064
2019	Spider	MC1	Flowering	Detritivore	0.005	0.005	0.003	0	0.018
2019	Spider	MC1	Ripening	Rice herbivore	0.985	0.011	0.988	0.956	0.998
2019	Spider	MC1	Ripening	Tourist herbivore	0.013	0.011	0.01	0.001	0.04
2019	Spider	MC1	Ripening	Detritivore	0.002	0.003	0.001	0	0.011
2019	Spider	MC2	Tillering	Rice herbivore	0.323	0.114	0.315	0.128	0.565
2019	Spider	MC2	Tillering	Tourist herbivore	0.101	0.063	0.089	0.016	0.251
2019	Spider	MC2	Tillering	Detritivore	0.576	0.136	0.58	0.297	0.824
2019	Spider	MC2	Flowering	Rice herbivore	0.924	0.039	0.93	0.832	0.979
2019	Spider	MC2	Flowering	Tourist herbivore	0.047	0.031	0.04	0.007	0.125
2019	Spider	MC2	Flowering	Detritivore	0.03	0.023	0.024	0.004	0.089
2019	Spider	MC3	Tillering	Rice herbivore	0.333	0.095	0.336	0.152	0.516
2019	Spider	MC3	Tillering	Tourist herbivore	0.415	0.088	0.41	0.252	0.609
2019	Spider	MC3	Tillering	Detritivore	0.252	0.117	0.237	0.064	0.518
2019	Spider	MC3	Flowering	Rice herbivore	0.82	0.074	0.832	0.646	0.93
2019	Spider	MC3	Flowering	Tourist herbivore	0.169	0.07	0.157	0.064	0.334
2019	Spider	MC3	Flowering	Detritivore	0.012	0.013	0.008	0.001	0.044
2019	Spider	MC3	Ripening	Rice herbivore	0.888	0.054	0.899	0.758	0.963
2019	Spider	MC3	Ripening	Tourist herbivore	0.106	0.052	0.096	0.034	0.234
2019	Spider	MC3	Ripening	Detritivore	0.006	0.008	0.003	0	0.026
2019	Spider	MO1	Tillering	Rice herbivore	0.217	0.114	0.199	0.055	0.498
2019	Spider	MO1	Tillering	Tourist herbivore	0.123	0.085	0.107	0.014	0.333
2019	Spider	MO1	Tillering	Detritivore	0.66	0.169	0.685	0.236	0.912
2019	Spider	MO1	Flowering	Rice herbivore	0.865	0.066	0.875	0.711	0.964
2019	Spider	MO1	Flowering	Tourist herbivore	0.078	0.046	0.071	0.014	0.189
2019	Spider	MO1	Flowering	Detritivore	0.057	0.052	0.042	0.004	0.192
2019	Spider	MO1	Ripening	Rice herbivore	0.923	0.047	0.935	0.8	0.984
2019	Spider	MO1	Ripening	Tourist herbivore	0.048	0.031	0.042	0.007	0.125
2019	Spider	MO1	Ripening	Detritivore	0.029	0.037	0.014	0.001	0.142
2019	Spider	MO2	Tillering	Rice herbivore	0.139	0.064	0.132	0.04	0.283
2019	Spider	MO2	Tillering	Tourist herbivore	0.053	0.038	0.044	0.006	0.149
2019	Spider	MO2	Tillering	Detritivore	0.808	0.081	0.814	0.629	0.939
2019	Spider	MO2	Flowering	Rice herbivore	0.854	0.072	0.866	0.687	0.959
2019	Spider	MO2	Flowering	Tourist herbivore	0.053	0.037	0.044	0.009	0.15
2019	Spider	MO2	Flowering	Detritivore	0.092	0.062	0.078	0.014	0.246
2019	Spider	MO3	Tillering	Rice herbivore	0.005	0.003	0.004	0.001	0.013
2019	Spider	MO3	Tillering	Tourist herbivore	0.497	0.186	0.464	0.218	0.947
2019	Spider	MO3	Tillering	Detritivore	0.498	0.186	0.531	0.048	0.779
2019	Spider	MO3	Flowering	Rice herbivore	0.054	0.03	0.048	0.014	0.126
2019	Spider	MO3	Flowering	Tourist herbivore	0.857	0.059	0.861	0.729	0.957
2019	Spider	MO3	Flowering	Detritivore	0.089	0.052	0.081	0.009	0.21
2019	Spider	MO3	Ripening	Rice herbivore	0.092	0.044	0.086	0.026	0.193

2019	Spider	MO3	Ripening	Tourist herbivore	0.842	0.068	0.851	0.683	0.951
2019	Spider	MO3	Ripening	Detritivore	0.066	0.058	0.049	0.003	0.214
2019	Spider	SC1	Tillering	Rice herbivore	0.229	0.093	0.229	0.057	0.412
2019	Spider	SC1	Tillering	Tourist herbivore	0.1	0.059	0.092	0.016	0.237
2019	Spider	SC1	Tillering	Detritivore	0.671	0.117	0.667	0.443	0.896
2019	Spider	SC1	Flowering	Rice herbivore	0.882	0.071	0.899	0.703	0.97
2019	Spider	SC1	Flowering	Tourist herbivore	0.066	0.046	0.054	0.011	0.186
2019	Spider	SC1	Flowering	Detritivore	0.052	0.048	0.038	0.007	0.181
2019	Spider	SC1	Ripening	Rice herbivore	0.933	0.051	0.947	0.798	0.989
2019	Spider	SC1	Ripening	Tourist herbivore	0.041	0.032	0.033	0.005	0.126
2019	Spider	SC1	Ripening	Detritivore	0.025	0.034	0.014	0.001	0.121
2019	Spider	SO1	Tillering	Rice herbivore	0.202	0.116	0.185	0.036	0.462
2019	Spider	SO1	Tillering	Tourist herbivore	0.101	0.074	0.085	0.012	0.286
2019	Spider	SO1	Tillering	Detritivore	0.698	0.145	0.71	0.391	0.929
2019	Spider	SO1	Ripening	Rice herbivore	0.917	0.066	0.936	0.747	0.988
2019	Spider	SO1	Ripening	Tourist herbivore	0.05	0.047	0.037	0.005	0.172
2019	Spider	SO1	Ripening	Detritivore	0.032	0.041	0.018	0.001	0.157
2019	adybeetl	LC1	Tillering	Rice herbivore	0.849	0.204	0.93	0.171	0.998
2019	adybeetl	LC1	Tillering	Tourist herbivore	0.071	0.164	0.012	0	0.716
2019	adybeetl	LC1	Tillering	Detritivore	0.08	0.126	0.028	0	0.472
2019	adybeetl	LC1	Flowering	Rice herbivore	0.884	0.16	0.94	0.406	0.997
2019	adybeetl	LC1	Flowering	Tourist herbivore	0.064	0.142	0.016	0	0.502
2019	adybeetl	LC1	Flowering	Detritivore	0.052	0.074	0.024	0	0.264
2019	adybeetl	LC1	Ripening	Rice herbivore	0.948	0.144	0.985	0.378	0.999
2019	adybeetl	LC1	Ripening	Tourist herbivore	0.037	0.141	0.004	0	0.611
2019	adybeetl	LC1	Ripening	Detritivore	0.014	0.025	0.006	0	0.083
2019	adybeetl	LC2	Tillering	Rice herbivore	0.831	0.225	0.925	0.112	0.999
2019	adybeetl	LC2	Tillering	Tourist herbivore	0.067	0.167	0.012	0	0.814
2019	adybeetl	LC2	Tillering	Detritivore	0.102	0.157	0.032	0	0.575
2019	adybeetl	LC2	Flowering	Rice herbivore	0.872	0.171	0.935	0.3	0.997
2019	adybeetl	LC2	Flowering	Tourist herbivore	0.063	0.142	0.016	0	0.588
2019	adybeetl	LC2	Flowering	Detritivore	0.065	0.096	0.027	0	0.346
2019	adybeetl	LC3	Flowering	Rice herbivore	0.88	0.16	0.935	0.344	0.997
2019	adybeetl	LC3	Flowering	Tourist herbivore	0.064	0.139	0.016	0	0.577
2019	adybeetl	LC3	Flowering	Detritivore	0.057	0.078	0.026	0	0.286
2019	adybeetl	LC3	Ripening	Rice herbivore	0.946	0.143	0.984	0.471	0.999
2019	adybeetl	LC3	Ripening	Tourist herbivore	0.038	0.139	0.004	0	0.473
2019	adybeetl	LC3	Ripening	Detritivore	0.017	0.028	0.006	0	0.099
2019	adybeetl	LO1	Ripening	Rice herbivore	0.94	0.138	0.981	0.46	0.999
2019	adybeetl	LO1	Ripening	Tourist herbivore	0.04	0.131	0.005	0	0.5
2019	adybeetl	LO1	Ripening	Detritivore	0.02	0.035	0.007	0	0.122
2019	adybeetl	LO3	Tillering	Rice herbivore	0.901	0.215	0.969	0.049	0.999

2019	adybeetl	LO3	Tillering	Tourist herbivore	0.054	0.179	0.007	0	0.891
2019	adybeetl	LO3	Tillering	Detritivore	0.045	0.121	0.015	0	0.493
2019	adybeetl	LO3	Ripening	Rice herbivore	0.958	0.154	0.993	0.242	1
2019	adybeetl	LO3	Ripening	Tourist herbivore	0.034	0.152	0.002	0	0.74
2019	adybeetl	LO3	Ripening	Detritivore	0.008	0.018	0.003	0	0.049
2019	adybeetl	MC2	Flowering	Rice herbivore	0.92	0.152	0.961	0.222	0.997
2019	adybeetl	MC2	Flowering	Tourist herbivore	0.05	0.146	0.011	0	0.708
2019	adybeetl	MC2	Flowering	Detritivore	0.03	0.037	0.017	0	0.137
2019	adybeetl	MC3	Flowering	Rice herbivore	0.872	0.163	0.93	0.352	0.997
2019	adybeetl	MC3	Flowering	Tourist herbivore	0.073	0.147	0.019	0	0.581
2019	adybeetl	MC3	Flowering	Detritivore	0.055	0.071	0.027	0	0.265
2019	adybeetl	MC3	Ripening	Rice herbivore	0.943	0.143	0.983	0.504	0.999
2019	adybeetl	MC3	Ripening	Tourist herbivore	0.04	0.139	0.005	0	0.466
2019	adybeetl	MC3	Ripening	Detritivore	0.017	0.029	0.006	0	0.1
2019	adybeetl	MO1	Ripening	Rice herbivore	0.92	0.165	0.98	0.346	0.999
2019	adybeetl	MO1	Ripening	Tourist herbivore	0.044	0.139	0.005	0	0.488
2019	adybeetl	MO1	Ripening	Detritivore	0.036	0.084	0.007	0	0.307
2019	adybeetl	MO2	Tillering	Rice herbivore	0.88	0.229	0.96	0.044	0.998
2019	adybeetl	MO2	Tillering	Tourist herbivore	0.081	0.219	0.008	0	0.917
2019	adybeetl	MO2	Tillering	Detritivore	0.039	0.068	0.018	0	0.185
2019	adybeetl	MO2	Flowering	Rice herbivore	0.901	0.185	0.964	0.142	0.998
2019	adybeetl	MO2	Flowering	Tourist herbivore	0.069	0.178	0.01	0	0.82
2019	adybeetl	MO2	Flowering	Detritivore	0.03	0.048	0.014	0	0.149
2019	adybeetl	MO3	Tillering	Rice herbivore	0.781	0.236	0.871	0.13	0.998
2019	adybeetl	MO3	Tillering	Tourist herbivore	0.092	0.179	0.018	0	0.736
2019	adybeetl	MO3	Tillering	Detritivore	0.126	0.172	0.049	0	0.625
2019	adybeetl	MO3	Flowering	Rice herbivore	0.826	0.185	0.886	0.271	0.996
2019	adybeetl	MO3	Flowering	Tourist herbivore	0.088	0.156	0.024	0	0.639
2019	adybeetl	MO3	Flowering	Detritivore	0.085	0.109	0.042	0	0.406
2019	adybeetl	MO3	Ripening	Rice herbivore	0.926	0.157	0.973	0.258	0.999
2019	adybeetl	MO3	Ripening	Tourist herbivore	0.05	0.151	0.007	0	0.665
2019	adybeetl	MO3	Ripening	Detritivore	0.024	0.037	0.01	0	0.129
2019	adybeetl	SC1	Flowering	Rice herbivore	0.892	0.161	0.947	0.297	0.997
2019	adybeetl	SC1	Flowering	Tourist herbivore	0.061	0.145	0.014	0	0.648
2019	adybeetl	SC1	Flowering	Detritivore	0.047	0.068	0.02	0	0.238
2019	adybeetl	SO1	Flowering	Rice herbivore	0.875	0.155	0.929	0.432	0.997
2019	adybeetl	SO1	Flowering	Tourist herbivore	0.065	0.133	0.018	0	0.475
2019	adybeetl	SO1	Flowering	Detritivore	0.06	0.079	0.028	0	0.287
2019	adybeetl	SO1	Ripening	Rice herbivore	0.943	0.139	0.982	0.546	0.999
2019	adybeetl	SO1	Ripening	Tourist herbivore	0.038	0.132	0.004	0	0.433
2019	adybeetl	SO1	Ripening	Detritivore	0.019	0.035	0.006	0	0.12

Declaration of interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

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3 **A predator in need is a predator indeed: generalist predators (spiders and
4 ladybeetles) specialize in pest consumption at the late growth stage of rice**

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18

Abstract

19 Biocontrol, using natural enemies for pest control, has a long history in agriculture. It has
20 received a surge of interest in the recent Anthropocene because of its potential as a valuable tool
21 for sustainable agriculture. To solve a long-standing puzzle in biocontrol—how well the
22 ubiquitous generalist arthropod predators (GAPs) function as biocontrol agents—this study
23 aimed to 1) quantify the diet composition of GAPs (spiders and ladybeetles) at different crop
24 stages using stable isotope analysis, 2) examine the consistency of GAPs in pest consumption
25 over years, and 3) investigate how abiotic and biotic factors affect pest consumption by GAPs.
26 Specifically, we sampled arthropod prey and GAPs in sub-tropical organic and conventional rice
27 farms over crop stages (seedling, tillering, flowering, and ripening) in three consecutive years.
28 Among our field-collected samples, 352 arthropod predator and 828 prey isotope samples were
29 analyzed to infer predator-prey interactions. Our results show the following: a) The proportion
30 of rice pests in GAPs' diets in both organic and conventional rice farms increased over the crop
31 season, from 21-47% at the tillering stage to 80-97% at the ripening stage, across the three study
32 years. The high percentage in pest consumption at late crop stages (flowering and ripening)
33 suggests that GAPs can function as specialists in pest management during the critical period of
34 crop production. Regarding individual predator groups, spiders and ladybeetles exhibited
35 distinct dietary patterns over crop stages. b) The high pest consumption by GAPs at late crop
36 stages was similar across years despite variable climatic conditions and prey availability,
37 suggesting a consistency in GAP feeding habits and biocontrol value. c) The proportion of rice
38 pests in GAPs' diets varied with farm type and crop stage (e.g., higher in conventional farms and
39 during flowering/ripening stages). By quantifying the diet composition of GAPs over crop
40 stages, farm types, and years, this study reveals that generalist predators have potential to

41 produce a stable, predictable top-down effect on pests in rice agro-ecosystems. As sustainable
42 agriculture has become increasingly important, incorporating the ubiquitous generalist predators
43 into pest management will likely open a promising avenue towards this goal.

44

45 *Keywords: biocontrol, trophic interactions, generalist predators, rice paddy, organic and*
46 *conventional farms, stable isotope analysis*

47 **1. Introduction**

48 Using natural arthropod enemies for pest control has a long history in agriculture. The
49 earliest record of biocontrol was documented in the book *Plants of the Southern Regions* (ca. 304
50 A.D.): people sold ants and their nests in the markets to control citrus insect pests (Huang and
51 Yang, 1987). While synthetic pesticides have become the main method for controlling pests in
52 the past century, this comes at a cost, such as posing risks to people, reducing biodiversity and
53 hampering ecosystem functions (Geiger *et al.*, 2010; Kehoe *et al.*, 2017). As agriculture has
54 become the largest land use type worldwide and a major driver for the global biodiversity crisis
55 in Anthropocene (Campbell *et al.*, 2017), a shift from synthetic pesticides to environmentally
56 friendly practices (e.g., biocontrol) is urgently needed to make agriculture more sustainable
57 (Gomiero *et al.*, 2011). For example, the European Commission has announced its plan to
58 reduce the use of chemical pesticides in European Union agricultural systems by 50% by 2030
59 (European Commission, 2020). To achieve this ambitious sustainability goal, biocontrol by
60 natural enemies has been considered a key approach and has regained importance in modern
61 agriculture.

62 Natural enemies used for pest control can be classified into two major groups based on
63 their prey range: specialist and generalist predators. While specialist predators (e.g., parasitoid
64 wasps) have been widely advocated in agriculture because they target specific pest species and
65 produce less undesirable non-target effects (Stiling and Cornelissen, 2005), generalist predators
66 (e.g., spiders) have been increasingly appreciated for their conspicuous existence and consistent
67 biocontrol effect on pests (Symondson *et al.*, 2002; Stiling and Cornelissen, 2005; Michalko *et*
68 *al.*, 2019; Hsu *et al.*, 2021; Gajski *et al.*, 2023). For example, generalist predators were
69 commonly reported in various agro-ecosystems and significantly reduced pest abundance in

70 approximately 75% of cases in 181 field manipulative studies (Symondson *et al.*, 2002).
71 Moreover, a meta-analysis suggests that generalist predators may exert stronger biocontrol
72 effects on pest populations over time compared to specialists (Stiling and Cornelissen, 2005).

73 While the value of generalist predators has been increasingly appreciated, a few
74 fundamental knowledge gaps need to be filled to validate their biocontrol potential and the
75 underlying mechanisms in agro-ecosystems. For example, while studies have qualitatively
76 analyzed the diets of generalist predators (e.g., using molecular gut content analysis to identify
77 prey species) (Eitzinger and Traugott, 2011; Ingrao *et al.*, 2017; Albertini *et al.*, 2018), very few
78 have quantified their diet composition over a growth season in the field (knowledge gap 1) (Hsu
79 *et al.*, 2021; Otieno *et al.*, 2023). Quantifying their diet composition will help address the
80 concern that generalist predators may switch their diet from pests to alternative prey and thus
81 reduce their pest control effectiveness (Michalko *et al.*, 2019). For instance, if generalist
82 predators still consume a high proportion of pests in their diet with the presence of alternative
83 prey in the field, this result would help end a long debate on whether generalist predators serve
84 well as biocontrol agents (Symondson *et al.*, 2002; Krey *et al.*, 2017; Michalko *et al.*, 2019).
85 Moreover, examining the consistency of generalist predators in pest consumption in the field
86 over years is important to assess the reliability of these predators as biocontrol agents in
87 agriculture, although this information is lacking (knowledge gap 2). Given that temporal
88 dynamics in population density or species composition commonly occur in agro-ecosystems
89 (Settle *et al.*, 1996; Dominik *et al.*, 2018), a consistently high pest consumption by generalist
90 predators over years, if it occurs, will provide strong support for applying these predators in pest
91 management programs.

92 To understand the underlying mechanisms for the biocontrol effect of generalist predators,
93 we also need to examine how various abiotic and biotic factors affect the diet composition of
94 generalist predators in agro-ecosystems (knowledge gap 3). First, arthropod community
95 composition (e.g., pest vs. alternative prey density) may vary with crop stages and affect
96 predator-prey trophic interactions (Roubinet *et al.*, 2017). Therefore, we should examine how
97 crop stage affects the pest consumption by generalist predators within a growth season. Second,
98 we should examine whether farming practices (e.g., organic and conventional) influence the diet
99 composition of predators (e.g., pest consumption) (Birkhofer *et al.*, 2011). This will demonstrate
100 whether generalist predators provide varying biocontrol values in specific farm types. Third, we
101 should investigate the relationship between the relative prey abundance and the diet composition
102 of their predators. This will clarify whether pest abundance or predator preference mainly
103 explains the pest consumption by predators (Wise *et al.*, 2006; Kuusk and Ekbom, 2012;
104 Roubinet *et al.*, 2017; Eitzinger *et al.*, 2019). Lastly, we should examine how surrounding
105 vegetation (e.g., forest cover) affects the diet composition of generalist predators. While
106 surrounding vegetation reportedly affected arthropod diversity and predator-prey interactions in
107 agro-ecosystems (Altieri and Letourneau, 1982; Altieri, 1999; Barbosa and Castellanos, 2005;
108 Diehl *et al.*, 2013; Lichtenberg *et al.*, 2017), its effect on predators' diet composition is unclear.
109 Understanding this will provide insights for managing the agricultural landscape and promoting
110 biocontrol services by generalist predators.

111 To address these three knowledge gaps, this study aimed to 1) quantify the diet
112 composition of generalist predators, 2) examine the consistency of predators in pest consumption
113 over years, and 3) investigate how abiotic and biotic factors may affect the diet composition of
114 these predators. Filling these gaps will provide insights for applying generalist predators in

115 biocontrol programs. Specifically, this study sampled arthropod prey and generalist arthropod
116 predators (GAPs) in sub-tropical organic and conventional rice farms over the rice growth season
117 (seedling, tillering, flowering, and ripening stages) in central Taiwan from 2017 to 2019, and
118 quantified the diet composition of GAPs (ladybeetles and spiders) at each rice stage using stable
119 isotope analysis ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$). Although GAPs may consume various prey items, we expected
120 that GAPs would consistently consume a high proportion of pests in their diet at late crop stages
121 (with high pest densities) regardless of years. We also expected that the diet composition of
122 GAPs would be affected by local abiotic and biotic factors (e.g., farm type, crop stage, percent
123 forest cover, and the relative abundance of pests in the field). Stable isotope analysis has been
124 widely applied in ecology to infer predator-prey trophic interactions and estimate the
125 proportional contribution of different prey sources to predators' diets (Post, 2002; Boecklen *et al.*,
126 2011; Layman *et al.*, 2012). This quantification method reflects accumulated prey consumption
127 in predators' diets, which may not be achieved by some "snap-shot" techniques (e.g., field
128 observations and molecular gut content analysis) (Newton, 2016).

129

130 **2. Materials and Methods**

131 *2.1. Study system and sample collection*

132 We collected terrestrial arthropods in paired organic and conventional rice farms in
133 subtropical Taiwan (120.656-120.721 °E; 24.364-24.489 °N) from 2017 to 2019 (three farm
134 pairs in 2017 and seven farm pairs each in 2018 and 2019). While farms in the same pair were
135 relatively close to each other (e.g., within a few hundred meters in distance), different farm pairs
136 were at least 1 km apart from each other to reduce confounding effects. The study farms were
137 0.2 hectares on average and irrigated with surface water. The organic farms were managed with

138 organic fertilizers (manure; 2-3 applications/crop season) and natural pesticides (tea saponins; 1
139 application/crop season during the seedling or tillering stage). The conventional farms were
140 managed with synthetic nitrogen fertilizers (2-3 applications/crop season) and organophosphate
141 pesticides (1 application/crop season during the tillering or flowering stage). At each major rice
142 crop stage (seedling, tillering, flowering, and ripening stages) during the growing season (April -
143 July) in each study year, we collected arthropod samples by sweep-netting (36 cm in diameter
144 with a mesh size of 0.2 × 0.2 mm) the crop canopy 30 times in each of two transects inside a rice
145 field. Each transect (ca 30 m long) was parallel to but 1.5m away from a randomly selected farm
146 ridge. Samples were sealed in bags without chemical preservatives, iced, and transferred to
147 refrigerator (-20°C) in the laboratory. We identified and counted arthropods under a dissecting
148 scope to the lowest possible taxonomic level (usually species, genus, or family). Main orders,
149 families, and genera have been documented in Hsu et al. (Hsu *et al.*, 2021).

150

151 *2.2. Stable isotope analysis of arthropod samples*

152 After identification, arthropod samples were prepared for stable isotope analysis. First,
153 samples were oven dried (50°C) for one week, ground, and weighed into individual tin capsules
154 (5 × 9 mm). If necessary, several conspecifics would be pooled into a capsule to meet the
155 minimum weight required for stable isotope analysis (i.e., 2 mg in this study). The number of
156 isotope capsules for each species generally mirrored the arthropod community composition in the
157 field. Stable isotope analysis (352 arthropod predator and 828 prey isotope samples) was
158 conducted at the UC Davis Stable Isotope Facility using a PDZ Europa ANCA-GSL elemental
159 analyzer interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd.,
160 Cheshire, UK). The standards for carbon and nitrogen stable isotope ratios were Vienna PeeDee

161 Beleminte and atmospheric N₂, respectively. The results of our samples were expressed in per
162 mil (‰) relative to the international standards ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$).

163

164 *2.3. Arthropod trophic guild assignment*

165 A trophic guild represents a group of species using similar resources and forms a basic
166 component of food webs. The concept has been proved to be practical in current ecology
167 because it condenses broad taxonomic information into distinct functional groups in
168 communities (Blondel, 2003). In this study, we classified arthropod samples into four trophic
169 guilds (one predator and three prey guilds): 1) “Predators” consisted of spiders and ladybeetles,
170 which are the primary GAPs in rice farms. 2) “Rice herbivores” consisted of major rice pests,
171 including planthoppers, leafhoppers, and stink bugs. 3) “Tourist herbivores” consisted of
172 herbivorous species without direct trophic association with rice plants, including some
173 grasshoppers and leaf beetles. 4) “Detritivores” consisted of arthropods that feed on decaying
174 organic material or plankton, including various midge and fly species. The classification of prey
175 guilds was based on a combination of literature surveys and k-means clustering of stable isotope
176 signatures of arthropod samples (see Appendix A: Fig. S1 for a stable isotope biplot for the three
177 prey sources). The arthropod families/genera in each trophic guild are detailed in Appendix A:
178 Table S1. This study focused on the trophic interactions between generalist predators and their
179 prey sources and therefore did not consider less abundant trophic guilds (e.g., parasitoids) in
180 subsequent analyses.

181

182 *2.4. Data analyses*

183 To quantify the diet composition of predators, we constructed Bayesian stable isotope
184 mixing models using the R MixSIAR package (Stock *et al.*, 2018) to estimate the proportions of
185 different prey sources (i.e., the three prey guilds including rice herbivores, tourist herbivores, and
186 detritivores) in predators' diet. In the mixing models, individual farm-year combination and crop
187 stage were included as fixed effects for predator isotope data; isotope data for the three prey
188 guilds were pooled respectively to generate fixed source values because of their high mobility
189 across farms (Mazzi and Dorn, 2012; Sun *et al.*, 2015). Isotope data at the seedling stage for the
190 three study years were omitted from the analysis due to insufficient sample sizes for model
191 estimation. To improve our model estimates, carbon and nitrogen concentration dependencies as
192 well as the residual/process errors were incorporated (Phillips and Koch, 2002; Stock and
193 Semmens, 2016). Trophic discrimination factors (TDFs) were estimated from the diet-dependent
194 discrimination equation proposed by Caut *et al.* (2009). We ran three Markov Chain Monte
195 Carlo (MCMC) chains, each with 50,000 iterations and a burn-in number of 25,000, along with a
196 non-informative Dirichlet prior. Chain convergence was assessed via Gelman-Rubin and
197 Geweke diagnostics. Bayesian posterior median estimates of diet composition (for each year-
198 farm-stage combination) were extracted for further analyses. Bayesian posterior means, SDs,
199 medians, and 95% credible intervals are provided in Appendix B.

200 To examine how local abiotic and biotic factors may affect the pest consumption by
201 GAPs, we fit weighted generalized linear mixed models (GLMMs) with a beta distribution and a
202 logit link function using the R glmmTMB package (Brooks *et al.*, 2017), with year, farm type,
203 crop stage, percent forest cover, and the relative abundance of rice herbivores as fixed effects,
204 farm ID nested within pair ID as random effects, and the proportion of rice herbivores consumed
205 in predators' diet as the response (i.e., posterior medians from the Bayesian stable isotope mixing

206 models). Weights were computed based on the number of diet estimates in each year. Model
207 parameters were estimated using maximum likelihood, and their significance was analyzed via
208 Wald chi-square test using the “ova” function in the R car package (Fox and Weisberg, 2018).
209 Tukey’s post-hoc tests ($\alpha = 0.05$) were performed for the significant factors using the “cld”
210 function in the R emmeans package (Length, 2018). The percent forest cover around each study
211 farm was estimated from Google Earth images by manually delimiting the forested areas within a
212 1-km radius circular buffer surrounding the farm and computing the fraction of these areas in the
213 buffer zone. The 1-km radius was based on previous studies (Rusch et al., 2016; Karp *et al.*,
214 2018). Because spiders and ladybeetles may have different feeding behavior and preference, we
215 also performed all the aforementioned analyses separately for each of the two predator groups.
216 All analyses were conducted in R version 4.0.3 (R Core Team, 2021).

217

218 **3. Results**

219 *3.1. Diet composition of predators in rice farms*

220 Across organic and conventional rice farms during 2017-2019, the proportion of rice
221 herbivores in predators’ diet increased over the course of the crop season from 21-47% at the
222 tillering stage to 80-97% at the ripening stage; the proportion of detritivores in predators’ diet
223 decreased from 35-61% at the tillering stage to <1% at the ripening stage; the proportion of
224 tourist herbivores in predators’ diet also decreased from 13-20% at the tillering stage to 3-18% at
225 the ripening stage (Fig. 1a; Appendix A: Table S2, Fig. S2).

226 Regarding individual predator groups, spiders and ladybeetles showed a marked
227 difference in their diet composition over crop stages during 2017-2019. Across organic and
228 conventional farms, spiders consumed a higher proportion of detritivores (31-55%) in their diet

229 in the beginning of crop season (tillering stage) and substantially increased the consumption on
230 rice herbivores to 78-95% in late crop season (ripening stage) (Fig. 1b; Appendix A: Table S2,
231 Fig. S2). In contrast, ladybeetles in both organic and conventional farms consumed a low
232 proportion of detritivores ($\leq 8\%$) and a steadily high proportion of rice herbivores ($\geq 80\%$) in
233 their diet throughout the crop season (Fig. 1c; Appendix A: Table S2, Fig. S2). Tourist
234 herbivores generally did not constitute an important prey source and contributed less than 33% to
235 the diet of spiders and ladybeetles (Fig. 1b, 1c; Appendix A: Table S2, Fig. S2).

236

237 *3.2. Patterns of rice herbivore consumption by predators*

238 We further analyzed rice herbivore consumption by GAPs since these herbivores are the
239 main pests of concern. The patterns of rice herbivore consumption by both predators in organic
240 and conventional rice farms were generally similar across the three study years, suggesting
241 consistency in GAPs' feeding habits (Fig. 2). Interestingly, spiders and ladybeetles exhibited
242 distinct within-season patterns of rice herbivore consumption. For spiders in organic and
243 conventional farms, the proportion of rice herbivores in their diet increased toward later crop
244 season, ranging from 17-48% (tillering) to 78-95% (ripening) (Fig. 2b; Appendix A: Table S2,
245 Fig. S2), whereas for ladybeetles in organic and conventional farms, the proportion of rice
246 herbivores in their diet remained relatively stable throughout the season, ranging from 80-93%
247 (tillering) to 97-98% (ripening) (Fig. 2c; Appendix A: Table S2, Fig. S2).

248

249 *3.3. Factors associated with rice herbivore consumption by predators*

250 The proportion of rice herbivores in GAPs' diet differed between organic and
251 conventional farms for both predators ($\chi^2 = 7.92, P = 0.01$) and spiders ($\chi^2 = 4.93, P = 0.03$), but

252 not ladybeetles ($\chi^2 = 0.47, P = 0.49$; Table 1). Specifically, both predators consumed a higher
253 proportion of rice herbivores in their diet in conventional vs. organic farms (Table 2). The
254 proportion of rice herbivores in GAPs' diet also differed among crop stages (both predators: $\chi^2 =$
255 $249.84, P < 0.001$; spiders: $\chi^2 = 119.01, P < 0.001$; ladybeetles: $\chi^2 = 184.32, P < 0.001$; Table 1).
256 Specifically, GAPs consumed higher proportions of rice herbivores in their diet at the flowering
257 and/or ripening stage vs. the tillering stage (Table 3).

258 The proportion of rice herbivores consumed in GAPs' diet was not associated with the
259 percent forest cover within a 1-km radius buffer surrounding the study farms (both predators: χ^2
260 $= 0.06, P = 0.80$; spiders: $\chi^2 = 0.12, P = 0.73$; ladybeetles: $\chi^2 = 0.34, P = 0.56$; Table 1).
261 Furthermore, the proportion of rice herbivores consumed was not associated with the relative
262 abundance of rice herbivores in the field (both predators: $\chi^2 = 0.56, P = 0.46$; spiders: $\chi^2 = 0.58,$
263 $P = 0.45$; ladybeetles: $\chi^2 = 0.38, P = 0.54$; Table 1).

264

265 **4. Discussion**

266 Because the worldwide demand for environmentally friendly practices in agriculture has
267 increased, we investigated the potential of GAPs (ubiquitous in nature) as biocontrol agents in
268 rice agro-ecosystems. Specifically, we used stable isotopes to quantify the diet composition of
269 GAPs in organic and conventional rice farms during the crop season in three consecutive years.
270 Our main results include the following: 1) Across the three study years, the rice herbivore
271 consumption by GAPs increased in both organic and conventional farms over the crop season,
272 from 20-47% at the tillering stage to 80-97% at the ripening stage. The high percentage at the
273 ripening stage indicates that GAPs could function as pest specialists during critical growth (late
274 crop) stages. Notably, rice herbivore consumption by spiders increased gradually toward the

275 later crop season, whereas the consumption by ladybeetles remained stable throughout the season.
276 2) Our results revealed similar among-year patterns in rice herbivore consumption by GAPs in
277 organic and conventional rice farms, suggesting a consistency in GAPs' feeding habits and
278 biocontrol value. 3) The proportion of rice herbivores in GAPs' diets varied with farm type and
279 crop stage (e.g., higher in conventional farms and during flowering/ripening stages). However,
280 contrary to results from previous studies, pest consumption by GAPs was not associated with
281 percent forest cover or the relative abundance of rice herbivores in the field. We discuss in the
282 following: 1) GAPs function as pest specialists at late crop stages, 2) GAPs exhibit consistent
283 pest consumption patterns over years, 3) factors associated with pest consumption by GAPs, and
284 4) the potential caveats of this study (e.g., pest suppression and intraguild predation). We finish
285 by highlighting the implications of our results for agricultural management.

286

287 *4.1. Generalist predators function as pest specialists at late crop stages*

288 While biocontrol, a farming practice with a long history, offers a promising solution for
289 sustainable agriculture, the use of GAPs as biocontrol agents remains a concern because GAPs
290 may switch diets between pests and alternative prey (Albajes and Alomar, 1999; Prasad and
291 Snyder, 2006; Roubinet *et al.*, 2018). This study addressed this concern and revealed a
292 consistency in high pest consumption by GAPs at late crop stages over years. The results
293 provide not only strong support for using GAPs in sustainable pest management, but also a novel
294 aspect in biocontrol—generalist predators may function as guild-level specialist predators of
295 pests during the late crop season. Specifically, across the three study years, GAPs in both
296 organic and conventional farms consumed an increasing proportion of rice herbivores over the
297 crop season, reaching 80-97% in predators' diet at the ripening stage, whereas the proportions of

298 alternative prey (detritivores and tourist herbivores) in their diet gradually decreased below 18%
299 at the ripening stage (Fig. 1; Appendix A: Table S2, Fig. S2). The increase in rice herbivore
300 consumption over time suggests that the biocontrol potential of predators increases toward late
301 crop stages and peaks at the critical stage of crop production. This could be because of a higher
302 herbivore (pest) density at late crop stages, suggested by a correlation between rice herbivore
303 consumption and crop stage (see *Factors associated with pest consumption by predators*).

304 While GAPs consumed a high proportion of pests at late crop stages, the two major
305 predator groups in our study system, spiders and ladybeetles (Table S1), exhibited distinct
306 dietary patterns over the crop season. Specifically, pest consumption by spiders increased
307 substantially, but pest consumption by ladybeetles remained stable over the season (Fig. 2b vs.
308 2c). This may be because different foraging modes—sit-and-wait (spiders) or actively hunting
309 (ladybeetles)—can lead to different prey capture and thus diet composition (Nyffeler, 1999;
310 Klecka and Boukal, 2013). For example, long-jawed orb-weavers (*Tetragnatha*), the most
311 abundant genus in our spider samples, are sit-and-wait predators. The diet composition of these
312 predators generally reflects prey availability (Nyffeler, 1999). In contrast, ladybeetles are
313 actively hunting predators and may preferentially feed on rice herbivores, resulting in stable pest
314 consumption over time. Because predator foraging modes shape predator-prey-plant interactions
315 (Schmitz, 2008), we encourage future studies to examine different assemblages of sit-and-wait vs.
316 actively hunting predators in field conditions to reveal the most efficient biocontrol practice over
317 the entire crop season.

318

319 *4.2. Generalists exhibit consistent pest consumption patterns over years*

320 Ideal biocontrol agents provide a consistent, predictable effect on pests under various
321 environmental conditions. Accordingly, GAPs in this study showed consistent pest consumption
322 across years, despite various abiotic and biotic environmental conditions. Specifically, regarding
323 the abiotic factors, the daily mean temperature, particularly from April to June, varied
324 substantially among years (Appendix A: Fig. S3). The daily precipitation also fluctuated over
325 the three study years, with multiple high precipitation events in 2017, overall low precipitation in
326 2018, and relatively uniform precipitation in 2019 (Appendix A: Fig. S3). Regarding the biotic
327 factors, the composition of rice herbivores at the flowering and ripening stages differed
328 substantially among the three years, in particular the two most dominant groups: leafhoppers
329 (*Cicadellidae/Nephrotettix*) and planthoppers (*Delphacidae/Nilaparvata*) (Appendix A: Table S3).
330 Although both abiotic and biotic factors varied substantially over the years of our study, pest
331 consumption by GAPs generally remained stable, suggesting that GAPs can be a predictable,
332 valuable tool for pest control in sustainable agriculture (but see Eitzinger *et al.*, 2021).

333

334 *4.3. Factors associated with pest consumption by predators*

335 The proportion of rice pests in GAPs' diets differed between farm types and among crop
336 stages but was not associated with the percent forest cover surrounding the farms or the relative
337 abundance of rice herbivores in the field. Overall, GAPs in conventional farms consumed a
338 higher proportion of rice pests in their diet compared to those in organic farms. There are two
339 explanations for this: 1) Organic farming may promote arthropod diversity and therefore distract
340 predators from feeding on target pests (Bengtsson *et al.*, 2005; Birkhofer *et al.*, 2008;
341 Lichtenberg *et al.*, 2017). 2) Pest densities may be higher in conventional farms (Porcel *et al.*,
342 2018), leading to higher predator-prey encounter rates and thus pest consumption by GAPs.

343 Regardless of the potential mechanisms, our results highlight the important but overlooked
344 biocontrol value of GAPs in conventional farming systems.

345 Besides farming practices, crop stages also affected pest consumption. Overall, pest
346 consumption by GAPs increased from early (tillering) to late (ripening) stages, consistent with
347 previous studies where predators consumed more pests in the late crop season (Roubinet *et al.*,
348 2017; Hsu *et al.*, 2021). This may be because pest populations increased with rice development
349 and eventually predominated, leading to high pest consumption by GAPs at the flowering and
350 ripening stages. These findings indicate a higher biocontrol value of predators when the crop
351 production is most vulnerable to pest damage. Therefore, farming practitioners may want to
352 avoid practices that harm predators (e.g., chemical applications) during this period to maintain
353 healthy predator populations and associated ecosystem services.

354 Complex habitat structure (e.g., surrounding vegetation) has been suggested to promote
355 predator abundance and diversity (Langellotto and Denno, 2004; Diehl *et al.*, 2013), but such
356 higher complexity did not affect predators' diet composition in our study. This might be because
357 the prey species in our study system were mostly associated with rice plants but not the
358 surrounding vegetation, consistent with a meta-analysis where habitat complexity had no effect
359 on crop herbivore densities (Langellotto and Denno, 2004). Furthermore, although the diet
360 composition of generalist predators may correlate with prey availability in the field (Wise *et al.*,
361 2006; Hsu *et al.*, 2021), our beta regression models suggest no such correlation between rice
362 herbivores and GAPs. An explanation is that the relative abundance of rice herbivores was
363 highly correlated with crop stage, a significant factor likely associated with various covariates
364 (e.g., rice plant height) and explaining most variations in pest consumption by GAPs . We

365 encourage further experiments, both observational and manipulative, to clarify the link between
366 prey availability and generalist predators' diet composition in the field.

367

368 *4.4. Potential caveats of this study*

369 Our study demonstrates high pest consumption by GAPs in rice fields over three years
370 and examines the factors influencing GAPs' diet composition. While our study provides
371 evidence for GAPs' biocontrol potential, some caveats may exist. First, high pest consumption
372 in GAPs' diets does not necessarily imply a strong suppression of pest populations in the field,
373 since pest population dynamics depend not only on the per capita effect of predators but also
374 predator density and diversity (Letourneau *et al.*, 2009; Rusch *et al.*, 2016). To unveil the
375 connection between per capita pest consumption and overall pest dynamics, future work may
376 require complementing stable isotope analysis with field observations of predator and pest
377 populations. Furthermore, future work may examine crop damage and production to reveal the
378 effect of GAPs on pest control and crop performance. Second, while intra-guild predation
379 potentially influences the pest control by GAPs (Straub *et al.*, 2008; Michalko *et al.*, 2019), it
380 was not quantified in our diet composition analysis due to the limitation of stable isotope mixing
381 models (Hsu *et al.*, 2021). However, this may not be a major concern in our study because rice
382 plants grow in dense clumps and form a complex structure that could substantially relax intra-
383 guild predation pressure (Finke and Denno, 2006; Janssen *et al.*, 2007). Regardless, we caution
384 that our diet estimates of predators (without predator-predator interference) might not apply to
385 systems where intra-guild predation prevails.

386

387 **5. Conclusions**

388 While biocontrol has been recognized as a valuable tool for sustainable agriculture,
389 whether generalist predators can serve as effective biocontrol agents in pest management remains
390 unclear. Our study helps solve this long-standing puzzle by using stable isotope analysis to
391 quantify the diet composition of GAPs (spiders and ladybeetles) over the rice growth season and
392 identifying the underlying mechanisms for enemy-pest interactions in rice farms over three
393 consecutive years. The results show a high proportion of rice pests in GAPs' diets in both
394 organic and conventional rice farms (e.g., 80-97% at the ripening stage), suggesting that these
395 generalist predators function as "pest specialists" at late crop stages (when rice plants are fruiting
396 and pests are abundant). The high pest consumption remained consistent across years regardless
397 of abiotic and biotic conditions, demonstrating the potential that generalist predators may
398 produce a stable, predictable top-down effect on pests. Overall, our study lends support to
399 applying generalist predators as biocontrol agents in both organic and conventional rice farms.
400 As sustainable agriculture has become more important than ever in human history, incorporating
401 the ubiquitous generalist predators into pest management, such as maintaining healthy
402 populations of these predators, will likely open a promising avenue towards this goal.

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408

409 **Declaration of competing interest**

410 The authors declare that they have no known competing financial interests or personal
411 relationships that could have appeared to influence the work reported in this paper.

412

413 **Data availability**

414 Data will be made available on request.

415

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421

422 **Author contributions**

423 All authors conducted the experiments; G.-C. Hsu and C.-K. Ho designed and wrote the
424 manuscript; G.-C. Hsu and J.-A. Ou performed the statistical analyses.

425

426 **Appendix A and B. Supporting information**

427 Supplementary information associated with this article can be found in the online version
428 at doi:xxx.

429

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- 585

586 **Table 1.** Statistical results from GLM beta regression models for examining the effects of
 587 abiotic and biotic factors on pest consumption by spiders, ladybeetles, and both predators.

588

589

Model	Factor	<i>d.f.</i>	χ^2	<i>P</i>
Both predators	Year	2	8.00	0.02
	Farm type	1	7.29	0.01
	Crop stage	2	249.84	< 0.001
	Percent forest cover	1	0.06	0.80
	Relative abundance of rice herbivores	1	0.56	0.46
Spiders	Year	2	9.30	0.01
	Farm type	1	4.93	0.03
	Crop stage	2	119.01	< 0.001
	Percent forest cover	1	0.12	0.73
	Relative abundance of rice herbivores	1	0.58	0.45
Ladybeetles	Year	2	17.29	< 0.001
	Farm type	1	0.47	0.49
	Crop stage	2	184.32	< 0.001
	Percent forest cover	1	0.34	0.56
	Relative abundance of rice herbivores	1	0.38	0.54

590

591

592 **Table 2.** Tukey's post-hoc tests comparing the proportion of rice herbivores consumed in the
 593 diet of predators in organic and conventional rice farms. Different superscript letters indicate
 594 significant differences in the estimated marginal means (EMMs) of the posterior medians from
 595 Bayesian stable isotope mixing models ($\alpha = 0.05$).

Model	Farm type	EMMs (\pm SE)	Lower 2.5%	Upper 2.5%
Both predators	Organic	0.61 ^a (± 0.08)	0.45	0.76
	Conventional	0.81 ^b (± 0.05)	0.69	0.90
Spiders	Organic	0.55 ^a (± 0.10)	0.35	0.73
	Conventional	0.79 ^b (± 0.07)	0.63	0.90
Ladybeetles	Organic	0.95 ^a (± 0.01)	0.93	0.96
	Conventional	0.95 ^a (± 0.01)	0.94	0.96

596

597

598 **Table 3** Tukey's post-hoc tests comparing the proportion of rice herbivores consumed in the
 599 diet of predators at three crop stages (tillering, flowering, and ripening stages). Different
 600 superscript letters indicate significant differences in the estimated marginal means (EMMs) of
 601 the posterior medians from Bayesian stable isotope mixing models ($\alpha = 0.05$).

Model	Crop stage	EMMs (\pm SE)	Lower 2.5%	Upper 2.5%
Both predators	Tillering	0.24 ^a (± 0.06)	0.14	0.36
	Flowering	0.85 ^b (± 0.04)	0.76	0.91
	Ripening	0.91 ^c (± 0.03)	0.85	0.95
Spiders	Tillering	0.27 ^a (± 0.07)	0.16	0.43
	Flowering	0.81 ^b (± 0.05)	0.69	0.89
	Ripening	0.86 ^b (± 0.04)	0.75	0.93
Ladybeetles	Tillering	0.92 ^a (± 0.01)	0.89	0.93
	Flowering	0.92 ^a (± 0.01)	0.90	0.93
	Ripening	0.98 ^b (± 0.01)	0.98	0.99

602

603 **Figures (color should be used for Figure 1, 2, and 3)**

604 **Figure 1.** The proportions (mean \pm SE) of prey sources (rice herbivores, tourist herbivores, and
605 detritivores) consumed in the diet of (a) both predators, (b) spiders, and (c) ladybeetles in organic
606 and conventional rice farms over crop stages. The proportions were computed from the
607 Bayesian posterior medians of diet estimates in replicate farms over the three study years.

608

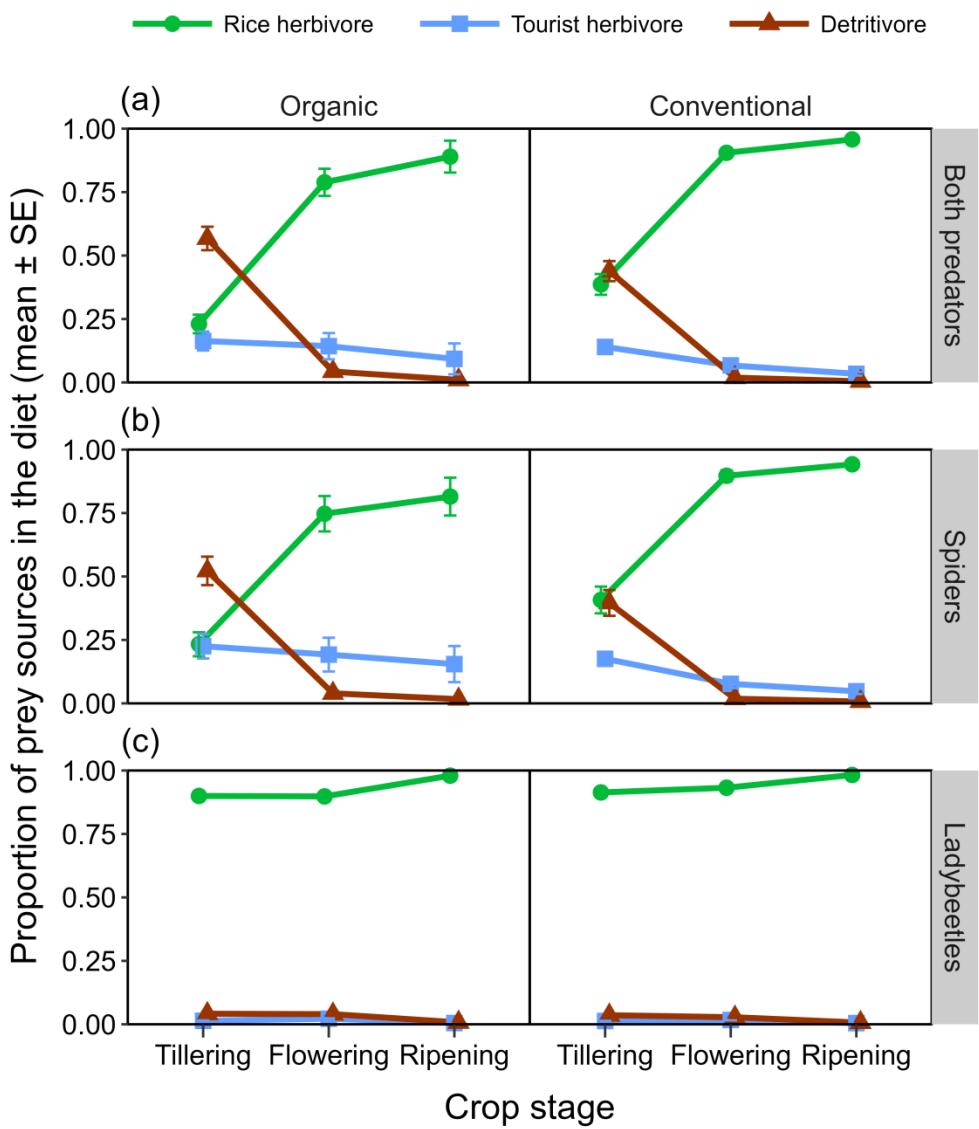
609 **Figure 2.** The proportion of rice herbivores consumed in the diet of (a) both predators, (b)
610 spiders, and (c) ladybeetles in organic and conventional rice farms over crop stages in the three
611 study years. The proportions were computed from the Bayesian posterior medians of diet
612 estimates in replicate farms.

613

614 **Figure 3.** The relative abundance of prey sources in organic and conventional rice farms over
615 crop stages during the three study years. The relative abundance was determined from the
616 sweep-net samples pooled across replicate farms.

617

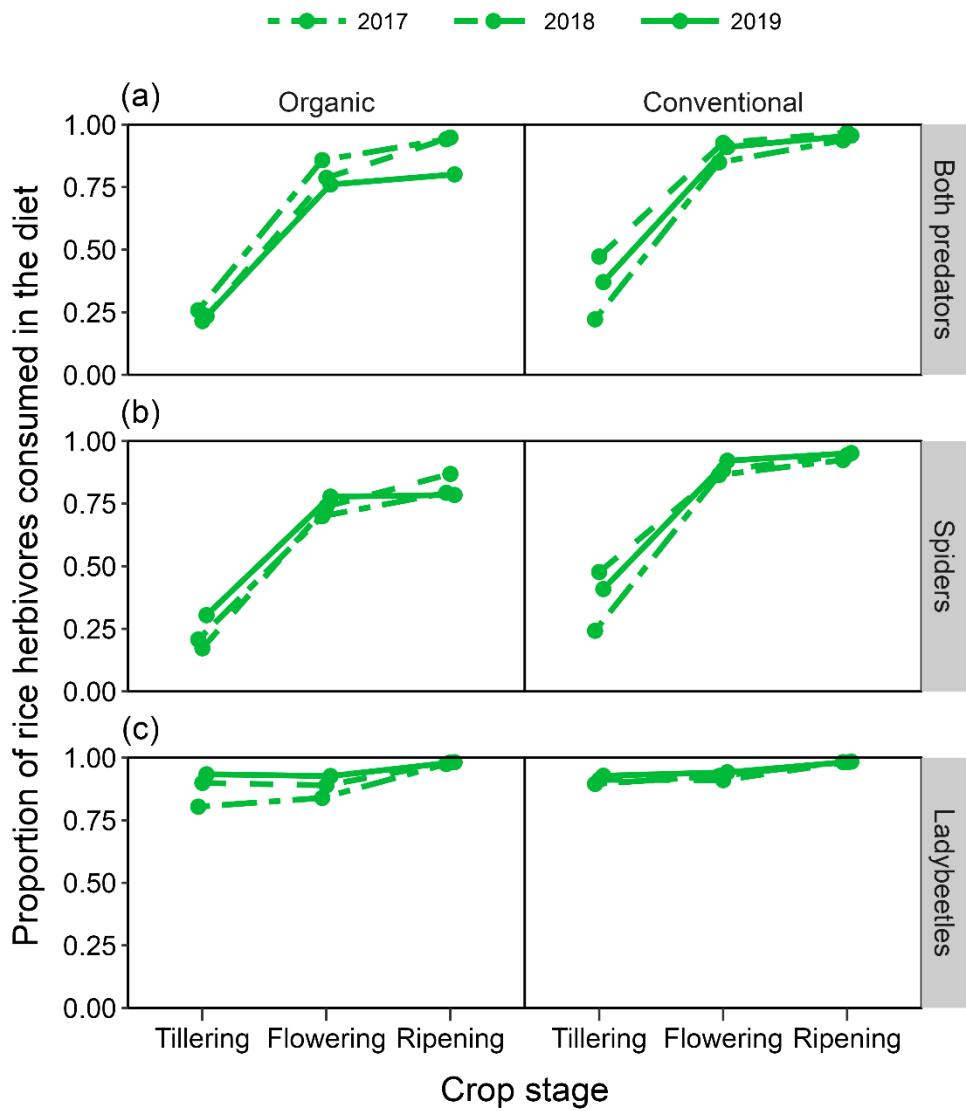
618 **Figure 1.**



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620

621 **Figure 2.**

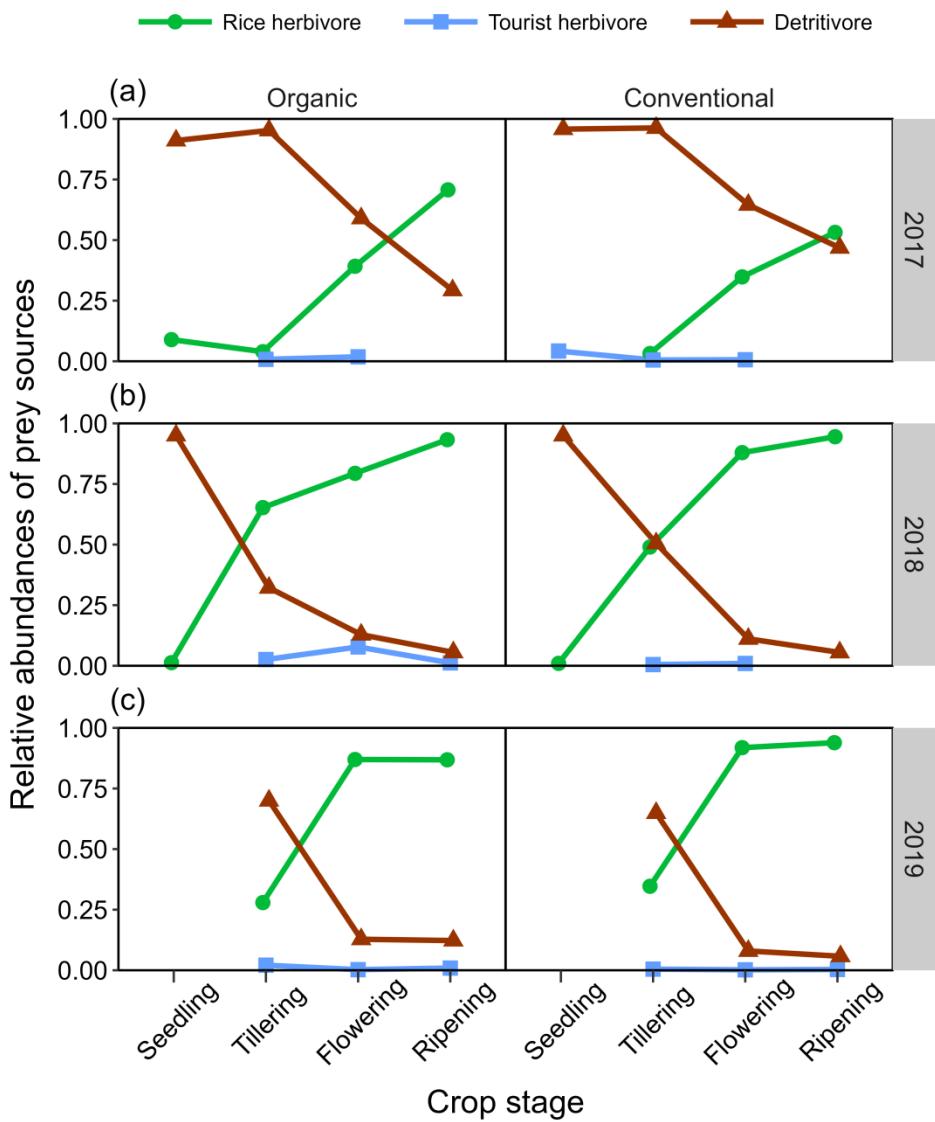


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625 **Figure 3.**



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